Fine-scale determinants of female grey seal (Halichoerus grypus) pupping site and habitat preferences at North Rona, Scotland.

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Abstract

The grey seal (*Halichoerus grypus*) is widespread in the Northern Hemisphere and throughout its range hauls out to breed terrestrially on a variety of substrates. A major breeding site in the eastern North Atlantic is the remote island of North Rona, Scotland, which is characterised by undulating grassy terrain, with limited access to the sea, punctuated by irregularly spaced fresh to brackish water pools of variable size. Previous long term research at North Rona has suggested that the distribution of breeding females is influenced by key habitat features including proximity to pools of water and to access from the sea. Using distributional information available for the North Rona colony in conjunction with a set of ecologically relevant environmental predictors within an extensive GIS database, the ecological niche of the grey seal at North Rona was modelled using Ecological Niche Factor Analysis. This was used to determine the distribution of suitable habitat at the North Rona colony and to elucidate the environmental determinants of female pupping site, and subsequent habitat, preferences over multiple years spanning 1998-2010. The environmental predictors utilised were chosen based on the conclusions of previous research. Following the delineation of basic environmental preferences, the influence of social interactions was considered within this modelling approach to further help explain the distribution of pups of various stages.

Adult female grey seals show a preference for both pupping sites and subsequent habitat near to pools of water of low salinity at intermediate distances to access points to the sea, though appear to exhibit stronger preferences regarding the characteristics of their habitat than pupping site. It is concluded that these preferences are a result of a requirement for proximity to pools for thermoregulation and for drinking water to avoid a negative water balance. However, females do not typically choose sites directly next to or within pools, this is a result of a trade-off between proximity to pools and proximity to their pup, which is at greater risk when separated from its mother, or close to pools in areas of high adult density. It also appears likely that females choose sites at intermediate proximity to access points as sites directly next to access points experience greater disturbance from other seals arriving to, or leaving, the colony. The widespread availability of apparently suitable habitat suggests that the North Rona colony is not restricted in size by limited availability of suitable pupping sites; other potential drivers of the decline of the North Rona colony are therefore discussed, with recommendations for future research. A parallel analysis investigating pup habitat use showed that weaned pups, unlike neonates, appear to avoid locations near to adult female grey seals. It is concluded that this is a result of social interactions driving weaned pups into areas abandoned, or not yet colonised, by adult females, which are aggressive towards conspecifics during lactation. Overall, the ENFA has provided an excellent means to assess the terrestrial pupping site and subsequent habitat preferences of the grey seal, though alternative approaches are suggested for also assessing social influences on space use.

Declaration of Copyright

I confirm that no part of the material presented in this thesis has previously been submitted by me or any other person for a degree in this or any other university. In all cases, where it is relevant, material from the work of others has been acknowledged. Fieldwork and initial GIS database development was carried out by Drs Sean D. Twiss and Paddy P. Pomeroy and aerial photography was conducted by Mr Callan D. Duck. All analyses were conducted by the author.

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Dedication

I would like to dedicate this thesis to my parents, Charles and Jacqui Stewart, who have been an inspiration to me, and for whose love, kindness and support I am forever grateful.

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1. Introduction

The aim of this chapter is to provide an introduction and background material to the concepts and techniques that form the basis of this thesis. Critical to this thesis is an understanding of habitat and organism-habitat relationships, a discussion of which leads to the definition of a species' niche and the concept of habitat selection (Section 1.1). Following an introduction to these key concepts, the issue of scale in habitat selection is discussed before methods are introduced for the quantification of the species-habitat relationship (Sections 1.3 and 1.4). The objectives of the research reported in this thesis are then outlined in Section 1.5, based on the background information supplied in Sections 1.1-1.4, though detailed information on the study species is contained mostly within Chapter 2.

1.1 Habitat, the ecological niche, and site selection

The concept of 'habitat' is central to the field of ecology, though the term is applied loosely to represent the concept at a range of spatial scales, including biome, ecosystem, community and foraging patch (Morris, 2003). As a result, 'habitat' can be associated with broad, landscape-scale (e.g. biome, ecosystem) or fine-scale (e.g. territory) descriptions of the environment (Block and Brennan, 1993). Odum (1971) proposed that the habitat of a species can be regarded as its "address", though debate typically surrounds the resolution of this "address" and, to extend the metaphor, whether it refers to the city, neighbourhood, street, house or room within the house that represents the best definition of habitat. Further confusion generally arises in the application of the habitat concept when additional terminology is introduced, for example "macrohabitat" or "microhabitat" (Block and Brennan, 1993). Habitat, and habitat selection, has therefore often been regarded in a hierarchical fashion, progressing from coarse, broad-scale descriptions to fine-scale descriptions of the environment (Johnson, 1980). Generally, the most appropriate definition of habitat depends on the population, species or community being studied, as well as the processes being investigated, as these determine the scale at which it is appropriate to define a habitat (see Sections 1.2 and 1.4.4 for further considerations of scale).

The study of habitat at a range of spatial scales has progressed through a series of three 'eras' defined by the links made between species and their environments (Block and Brennan, 1993). The first of these three eras was the "catalogue" era, which began around the time of Aristotle (Mayr, 1982) and progressed up until the early twentieth century. During this time basic relationships were observed and associations formed between animals and their general environment, a practice characterised by the work of John Audubon on birds (Audubon, 1832). The pioneering work of Charles Darwin (1859), highlighting the concept of natural selection and the adaptations of organisms to their environment, induced naturalists to go beyond simple

qualitative descriptions of species-habitat relationships, and to think about the evolutionary basis for these relationships. This new approach signalled the beginning of the second era, one focused on qualitative natural history (Block and Brennan, 1993). At the forefront of this approach was Joseph Grinnell, who applied Darwinist views to speculate on the environmental factors influencing species distributions (e.g. Grinnell, 1904). Grinnell's approach and ideas during this era lead to the formulation of one of the earliest descriptions of species-habitat relationships, now known as the 'Grinnellian niche' (Grinnell, 1917). Grinnell's definition of a species' 'niche' was based on the focal species' environmental requirements, which were seen as the basis for the species' spatial distribution. The definition of niche was later revised to include biotic factors, such as heterospecific presence, in the potential predictors of a species' distribution (Elton, 1930), a definition known as the 'Eltonian niche'.

In the early 20th century it was suggested that it might be possible to predict species presence, absence and abundance based on habitat information (e.g. Lack, 1933), though neither the general definition of habitat, nor the Grinnellian or Eltonian definitions of the niche provided a quantitative basis for investigating species-habitat relationships, or provided any predictive power. The contemporary approach to the study of the species-habitat relationship was shaped in the current "quantitative ecology" era (Block and Brennan, 1993) by G. Evelyn Hutchinson and Robert MacArthur (Hutchinson, 1957; MacArthur, 1958). Hutchinson (1957) was the first to move towards a more quantitative approach, providing a quantitative definition of the niche concept which described the *fundamental* niche as a hypervolume envelope plotted on a set of *n*-dimensional resource axes which encompasses the coordinates of all conspecific individuals. These axes should describe the complete range of the various environmental conditions that are ecologically relevant to the life history of that species, and therefore its distribution, and should be independent of one another. The fundamental niche, therefore, encloses the range of environmental conditions within which a population can persist, presumably without immigration (i.e. can exist without supplementation from neighbouring populations). The *realised* niche is a subset of this hypervolume, and represents the restriction of the fundamental niche by heterospecific interactions which limit the actual distribution of the species. In this sense, the Hutchinsonian definition is a synthesis of the Grinnellian and Eltonian definitions, encompassing both the behavioural (biotic) and physical (abiotic) classes of variable that influence the species' distribution. MacArthur's 1958 study of five warbler species applied the niche concept to quantify and elucidate fine-scale differences in species distribution, noting interspecific differences in distribution across parts of a tree. A brief lag followed this study before multivariate statistics became more widely applied to quantify species-habitat relationships, using computers to cope with the computational burden of these more complex analyses (e.g. Cody, 1968; James, 1971; Noon, 1981; Sections 1.3 and 1.4).

Regardless of the definition of 'niche', it is often clear that species generally show affinities for particular environmental characteristics, and that these affinities may be thought of as a species' preferences for particular conditions. Expression of these preferences leads directly to the concept of habitat selection and often results in the species' distribution being considerably narrower than their fundamental niche (Colwell and Fuentes, 1975). A hierarchical framework to the process of habitat selection was proposed by Johnson (1980), based on the four hierarchical scales at which habitat selection could be considered. First-order selection defines the geographical range of the species, and therefore represents the coarsest scale. Within this range, the scales become progressively finer, through individual or group home ranges (second order) to sites within a home range (third order), to the resources acquired within the site (fourth order). It is likely that first-order selection is largely innate and inflexible, constrained by limits to dispersal, whilst the finer orders of selection represent decision-making processes that can be influenced by an individual's perception of, and response to, their environment (Hutto, 1985). Within the third and fourth orders of selection, the scale at which habitat selection can be said to occur will depend largely on the grain of perception of the focal species; this will be considered further in Sections 1.2 and 1.4.4.

Habitat selection behaviour is likely to be subject to natural selection (Partridge, 1978): when animals must choose a site within a heterogeneous landscape that is spatially and temporally variable it is expected that the various options will differ in their fitness costs and benefits, and the choice will, therefore, have an effect on the fitness of the individual. Under this assumption, it is hypothesised that species "ideally" would use the highest quality habitat first, and disperse to lower quality habitats based on the density of individuals at each site (Fretwell and Lucas, 1970). The "Ideal Free Distribution" (IFD) model of Fretwell and Lucas (1970) depends on three basic assumptions; firstly, that habitat quality decreases with increasing density of occupants, secondly, that organisms select the habitat that confers the greatest fitness benefit, based on an ideal knowledge of all available habitats and the density of conspecifics in those habitats and, lastly, an organism is free to choose between all of the options. Therefore, the density of individuals in each patch will be proportional to the quality of the patch, based on the available resources. This model was originally conceived with reference to the choice of nesting habitat in birds, but has since been applied to other diverse animal and plant taxa (e.g. Tregenza, 1994; Gersani *et al.,* 1998). It has since been recognised that assumption of "free" movement and choice of habitats is not always met, particularly where territorial behaviour of conspecifics prevents entry to, or movement amongst, alternative patches. The Ideal Despotic Distribution (IDD) model takes the order of settling into account, accounting for such territoriality (Fretwell, 1972). The IFD and IDD provide a useful foundation for explaining a species' distribution on the basis of individual decisions, and link these decisions to patch quality, with assumed fitness

consequences which demonstrate the ecological importance of habitat selection. These fitness consequences arise through trade-offs between various costs and benefits related to factors that limit or enhance site quality, including basic abiotic determinants such as water and shelter availability. These trade-offs may include territoriality and competition, as outlined by the IDD, or factors such as predator presence, which can affect movement and habitat use (Connell, 1975), or disease, which has been theoretically shown to influence habitat selection patterns (Robertson and Hamilton, 2012). Conspecific attraction is likely to be important here, particularly in colonially breeding species, as it may increase the risk of disease transmission, but may also lead to higher breeding densities that might protect against predation (e.g. Schädelin *et al.,* 2012).

Most theories of habitat selection do not consider the associated costs (Morris, 2003), though these are likely to provide important contributions to the associated fitness trade-offs, and are frequently demonstrated empirically (e.g. Gilliam and Fraser, 1987; Pettorelli *et al.,* 2005; McLoughlin *et al.,* 2006; Titeux *et al.,* 2007). For example, dispersal costs are likely to increase with distance from the organism's current location and likely set an upper limit to the scale of habitat selection (Morris, 1992), whilst habitat selection based on predator avoidance may be associated with decreased food intake (Holomuzki, 1986; Gilliam and Fraser, 1987). Although the acquisition of high quality resources presents an obvious benefit to an organism that is "ideal" in its knowledge of available habitat patches, there are occasions on which a dispersing organism may incorrectly assess patch quality. This maladaptive habitat selection results from imperfect perception or knowledge of a site, which may arise due to difficulty in detection of factors leading to high rates of mortality or breeding failure. Maladaptive habitat selection is especially likely in areas undergoing rapid environmental change, which reduces site quality before it can be perceived by settlers, turning the area into an 'ecological trap' as a result of the decoupling of habitat quality and the cues used by animals as indicators of quality (Robertson and Hutto, 2006). Alternatively, occupation of these 'sink' habitats may be a result of density-dependent interference competition for the high quality 'source' habitats forcing subordinates to disperse to the next-most preferred sites (Delibes *et al.,* 2001).

Clearly then, the process of habitat selection is vital to determining the fitness outcome of an organism presented with a heterogeneous landscape. The choice expressed by each individual may then be interpreted as its habitat preferences given the information available about the environment, and the restrictions imposed by other organisms. Assuming a similar process for each individual in a population, the environmental characteristics associated with each individual's geographical location can be analysed in order to assess the set of environmental characteristics that lead to the distribution of the species (Araújo and Guisan, 2006). This has been the aim of many ecological studies in recent decades, increasing in depth and detail alongside the development of increasingly complex statistical and computational techniques that

allow for accurate quantification and assessment of species preferences. These studies investigate the habitat characteristics of locations used by the species in comparison to those areas that are unused or, more commonly, the areas that are available to the species (Manly *et al.,* 2002). Where a habitat is used disproportionately to its availability, this habitat is said to be 'selected for', and avoided where the proportion of use is lower than the proportion available. In order to accurately study the relationship between a species' distribution and habitat characteristics such as topography, it is important to quantify the habitat at a relevant spatial scale.

1.2 The importance of scale

There are two important components to scale in ecological studies: grain and extent (Forman and Godron, 1986; Wiens, 1989). Extent refers to the range at which features relevant to the distribution of an organism can be distinguished by the focal organism, whilst the grain refers to the finest discernible component of the environment. Extent is important as it defines the habitat available for an organism to choose from, and will therefore affect the outcome of use *versus* availability comparisons, whilst grain is important as it determines the resolution at which changes in the environment may be seen to affect the focal species. Ideally both grain and extent would be defined objectively from the focal species' point of view (Kolasa and Rollo, 1991) and would therefore be dependent on the organisms' degree of perceptual (e.g. visual) acuity, but is often performed subjectively due to the difficulties inherent in assessing the organism's perceptive abilities. In fact, both grain and extent are often defined by the availability and quality of data, though in the collection of data, where possible, it is important to collect data at a spatial grain that is considered relevant to the focal species. Furthermore, both are dependent upon which of Johnson's scales of selection are being assessed (Johnson, 1980). At the first and second order of selection, the grain may be rather coarse as organisms (e.g. migratory or dispersing individuals) choose between large-scale geographic regions. However, at the third and fourth orders of selection, the spatial grain is likely to be much finer and, in practical terms, is best defined by the scale at which habitat features affect the individual. For example, where variable topography results in differential costs of movement between areas, it would be desirable to measure the topography with a grain based on the smallest degree of change that affects movement costs. Studies incorporating this level of detail require detailed mapping data, the collection, manipulation and analysis of which has been enabled by advances in technology such as Geographic Information Systems (GIS).

1.3 Geographic Information Systems

A GIS is a computer-based system used to collect, store, update, visualise and analyse spatial data. A GIS may therefore be used to quantify the location of objects that one is interested

in, in addition to storing supplementary information about these objects. For example, it is possible to record the presence of individual organisms as X,Y map coordinates representing real-world locations on the Earth within a *point 'coverage'*, in addition to labelling these individuals with known information such as identities, age or sex. These points (or lines or polygons, depending on the format chosen) can then be linked with additional layers using the same coordinate system in order to associate the features of interest with ecogeographical variables (EGVs) such as the slope, soil moisture or acidity of a location. Point data on the distribution of organisms can therefore be associated with various layers that describe relevant characteristics of the environment, which may be useful predictors of the species' distribution. The analytical techniques afforded by GIS technology therefore allow a more precise quantitative approach to defining habitat preferences. Rather than defining preferences based on measures of central tendency at *qualitatively* described sites, as was previously common in ecological studies (Johnston, 1993), it is possible to analyse the spatially and temporally heterogeneous distribution of resources and individuals within an accurate representation of the habitat in question. Several multivariate statistical approaches, collectively referred to here as Species Distribution Modelling (SDM) approaches, are now available which operate in conjunction with a GIS in this way to characterise and predict species distributions based on the location of a species relative to the distribution of key EGVs (Guisan and Zimmerman, 2000). When this approach is taken, generally all GIS layers, whether point, line or polygon coverages, are converted to raster grid format, which presents the data as grids of *N* isometric cells covering the entire study area. Where possible, all raster grids should be the same size and cell resolution; the use of data in this format allows direct overlays of different data layers, giving effective comparisons.

1.4 Species Distribution Modelling

1.4.1 An introduction to Species Distribution Modelling

Here I will describe the concept of SDM and give a brief overview of common methods and applications. However, it is beyond the scope of this thesis to synthesise the theory, advantages and disadvantages of each approach. Instead, the choice of modelling approach used in this thesis is explained in detail in Section 4.2, and the advantages and disadvantages of this approach relative to others available is discussed in Sections 4.2 and 4.4. A history of the SDM literature and a more in-depth discussion of the technical details of each approach are provided elsewhere (e.g. Guisan and Zimmerman, 2000; Elith *et al.,* 2006; Elith and Leathwick, 2009).

SDM is increasingly being used alongside GIS to delimit population distributions, resource availability and habitat utilisation (Elith and Leathwick, 2009). The variety of SDM approaches is mirrored by the variety of names applied to them, including: species distribution models, habitat suitability (HS) models, ecological niche models, bioclimatic models, resource selection functions

and correlative models (Elith and Leathwick, 2009). Often these names refer to approaches which differ slightly from other approaches, but they all essentially relate species distribution data (occurrence or abundance at known locations) to the ecological and geographical characteristics (EGVs) of these locations. For simplicity, SDM will be used as an umbrella term to refer to all of these approaches. The utility of SDMs has been made clear by their increasing use in a range of applications (Table 1.1). SDMs are especially useful because it is often possible to extrapolate the niche model or HS output to areas for which the researcher has spatial environmental data but no species distribution data. This is a common problem which tends to arise due to the logistical difficulty or cost of performing adequate species sampling at all sites of interest. Thus, research findings can be applied more broadly to predict potential species distributions and aid the search for likely populations (Gibson *et al.,* 2004) or identify areas of high and low suitability for the focal species (e.g. Hirzel *et al.,* 2001). Indeed, there has generally been a gradual shift in SDM application towards this predictive objective, driven largely by increased demand for mapped products for conservation and land management (Elith and Leathwick, 2009), whereas earlier studies focused more on applying SDMs to gain ecological insight into determinants of species distributions (Mac Nally, 2000). Despite this general shift, SDMs are still commonly applied purely to seek insight, particularly in quantitative ecological studies, such as that presented here, and in evolutionary biology, integrating SDMs with a phylogenetic approach to explore speciation (Leathwick and Austin, 2001; Graham *et al.,* 2004).

Table 1.1: Summary of some applications of species distribution modelling, with example references.

Application	Example reference
Management strategies for	
- Threatened species	Osborne *et al.* (2001)
- Invasive species	Roura-Pascual *et al.* (2011)
Population Viability Analyses	Akçakaya and Atwood (1997)
Species re-introductions	Hirzel *et al.* (2004)
Ecosystem restoration and landscape management	Mladenoff *et al.* (1997)
Reserve and reserve network design	Bani *et al.* (2002); Araújo *et al.* (2004)
Assessing and managing impacts of climatic and anthropogenic disturbance	Le Lay *et al.* (2001); Araújo *et al.* (2004); Gilles *et al.* (2011)
Increase knowledge of species	Raxworthy *et al.* (2003)
Assess areas of ecological importance for a species	Suarez-Seoane *et al.* (2002)

There is now a multitude of multivariate statistical approaches (SDM techniques) available which operate in conjunction with a GIS to define habitat preferences and predict species distributions based on EGV and species distribution data (Guisan and Zimmerman, 2000). These techniques vary in how they model the response, select, weight, and allow for interactions between relevant EGVs and predict occurrences in geographic space (Elith *et al.,* 2006). A major distinction between these lies in the type of distribution data that they utilise: presence-only (PO)

or presence/absence (PA) data. These broad classifications are useful as a basis for outlining the available techniques, as the type of data available is a major determinant of the approach chosen.

1.4.2 Presence/absence data

Most common SDM techniques rely on the use of PA data (e.g. logistic regression or classification and regression trees; Guisan and Zimmerman, 2000; Segurado and Araújo, 2004). The most frequently used SDM approach is Generalised Linear Modelling (GLM; Rushton *et al.,* 2004), though Generalised Additive Models (GAMs) are in increasing use (Thuiller, 2003). Their popularity may be largely due to their ease of implementation within a GIS (Guisan *et al.,* 1998), and both are used extensively. These regression-based approaches relate PA data to a single (simple regression) or a combination (multiple regression) of EGVs (Guisan and Zimmerman, 2000). Additional regression techniques include boosted regression trees (BRT; Elith *et al.,* 2006) and multivariate adaptive regression splines (MARS; Leathwick *et al.,* 2006; Elith and Leathwick*,* 2007). Alternative, non-regression-based, PA techniques include Artificial Neural Networks (ANN, implemented in the software SPECIES; Pearson *et al.,* 2002). Like ANN, many other techniques have been implemented within freely available software; for example, BIOMOD software incorporates multiple PA methods including GAMs and GLMs (Thuiller, 2003), whilst all regression techniques identified above are implemented in R (R Development Core Team, 2012).

In some instances, the utilisation of PA techniques has been shown to improve model performance over that achieved by PO techniques (Brotons *et al.,* 2004). Therefore, where absence data have not been explicitly collected, some authors recommend using "pseudo-absence" data in order to make use of the PA framework (Osborne *et al.,* 2001; Stockwell and Peterson, 2002). This is performed primarily to avoid the situation whereby a lack of absence data leads to overly 'optimistic' model output due to the lack of restrictions which might otherwise be imposed upon the modelled niche of the species by absence data (Brotons *et al.,* 2004). In this approach, PO data are supplemented with pseudo-absences generated in one of three ways: (i) randomly choosing points from across the entire study site to represent absences (e.g. Stockwell and Peters, 1999); (ii) selecting random absence points as in (i) but weighting them in favour of those areas confirmed to contain 'true' absences (Zaniewski *et al.,* 2002); (iii) including absence points identified from a circular buffer area around each presence point (Hirzel *et al.,* 2001). Techniques such as genetic algorithm for rule-set prediction (GARP; Stockwell and Peters, 1999) can be applied using this presence/pseudo-absence data, whilst the PA methods outlined above can also be used. However, it is important to note that using presence/pseudo-absence data with techniques such as GLMs and GAMs can lead to weaker predictions than the same model using PA data (Ferrier and Watson, 1997; Engler *et al.*, 2004; Pearce and Boyce, 2006).

When absence data are unreliable, PA approaches are at risk of incorporating 'false absences', which have been shown to bias regression models even at low levels of non-detection (Gu and Swihart, 2004). The focal species may be absent from a location for one of three reasons: (i) the species was present but could not be detected at the time of surveying (Kéry, 2002) (ii) the habitat is suitable yet the species is absent for historical reasons including, but not limited to, colonisation patterns and dispersal (Svenning and Skov, 2004) (iii) the species is absent because the habitat is truly unsuitable. This last situation is the only case of a 'true' absence, and the previous two cases characterise 'false' absences. These false absences will not only bias normal PA models, but will also bias the pseudo-absences generated from background areas in which there are no species presences. Therefore species absence data can provide a confounding indicator with no clear link to habitat quality or suitability. Unreliable absence data could therefore impose severe limitations to the effective use of PA approaches. For this reason, Guisan and Zimmerman (2000) and Austin (2002) stressed the need for application of sound ecological knowledge of the focal species in the decision of which approach to utilise, particularly with regards to the species' prevalence and tolerance of environmental change (Hirzel *et al.,* 2001; Brotons *et al.,* 2004). Numerous authors have therefore advocated the use of PO-based approaches in such cases (Hirzel *et al.,* 2001; Pearce and Boyce, 2006; Elith *et al.,* 2006).

1.4.3 Presence-only data

Though PO approaches have been grouped together here, there are technically two approaches to producing a SDM with PO data. The first relies solely on presence records, without reference to other samples from the study area; examples include the Gower metric, implemented in the software DOMAIN (Carpenter *et al.,* 1993). Data in this format has most commonly been analysed using environmental envelope approaches, particularly using software such as BIOCLIM (Busby, 1991) and HABITAT (Walker and Cocks, 1991), though recent advances in support vector machines for one-class problems (SVM; Guo *et al.,* 2005) represent more flexible refinements of these approaches. Envelope approaches identify a multidimensional environmental envelope, which is almost analogous to Hutchinson's "hyperspace" (Hutchinson, 1957), containing all data points; the characteristics of the envelope can then be used to define species-habitat associations and predict potential distributions. The second approach uses 'background' environmental data from the entire study area, focusing on how the environment at species locations differs from that available over the study area as a whole (the 'background'). Examples include Ecological Niche Factor Analysis (ENFA, implemented in the software BioMapper; Hirzel *et al.,* 2002), Maximum Entropy (implemented in the software MAXENT; Phillips *et al.,* 2006) and Principal Components Analysis (PCA, implemented in R and BioMapper; Legendre and Legendre, 1998; Hirzel *et al.,* 2002). It is important to note that species locations are also included in the 'background', as these still represent available sites. Techniques such as GARP

are often regarded as PO approaches; however, these were considered in Section 1.4.2 as they require the generation of pseudo-absences and so technically use a form of PA data.

The purpose of this review was not to discuss each approach in any detail, but to highlight the importance of the format taken by the input species distribution data. There has been considerable debate as to which approach (PA or PO) is most effective in different situations (Brotons *et al.*, 2004; Hirzel *et al.*, 2001), with numerous studies attempting to compare the results of multiple techniques applied to similar datasets. For example, Hirzel *et al.* (2001) compared GLM with ENFA based on data from a 'virtual' species with simulated distribution data (thus allowing the authors to assess model performance compared to the 'truth'). Similar studies have been performed using real data collected in the field (e.g. Brotons *et al.,* 2004; Elith *et al.,* 2006). Brotons *et al.* (2004) concluded that PA approaches perform better than PO approaches where absence data are reliable and therefore contribute usefully to model calibration, especially for wide-ranging and tolerant species (where tolerance refers to tolerance of a wide range of environmental conditions, or environmental change). However, as noted above, where absence data are unreliable PA approaches are at risk of incorporating 'false absences', which are likely to introduce considerable bias (Gu and Swihart, 2004). Unreliable absence data is a common occurrence in ecological studies (Hirzel *et al.,* 2002), particularly for poorly known or cryptic species, or species not at equilibrium with their environment (i.e. not occupying all suitable areas); for example, Kéry (2002) found that 34 unsuccessful site visits were required to assert with 95% confidence that the snake *Coronella austriaca* was absent. Sources of PO data are widespread and include atlases, museum and herbarium records, incidental observation databases, radio-tracking studies and species lists (Pearce and Boyce, 2006). These data sources are likely to be vital to conservation projects that require a description of a focal species' distribution and habitat use but which do not have the funding or logistical capabilities to collect reliable PA data. This is especially likely where the focal species is rare, highly mobile or otherwise difficult to detect. Therefore, appropriately chosen and applied PO approaches can be useful in a range of situations in which PA approaches are not applicable.

1.4.4 Applying SDMs: The importance of scale

Though the choice of PA or PO approach is important in any SDM study (Sections 1.4.2 and 1.4.3), the choice of scale and of appropriate EGVs (predictor variables) is also important. The importance of scale was outlined in Section 1.2, and the implications of coarse- *versus* fine-scale data are addressed in greater detail elsewhere (see Elith and Leathwick, 2009, and references therein). However, in reviews of this issue, authors typically agree that there is no single scale at which it is best to study ecological relationships. Like the choice between PA and PO approach, the choice of scale is largely dependent upon the questions being asked (Levin, 1992; Elith and Leathwick, 2009). For example, the purpose of the analysis is generally reflected in the extent

(Elith and Leathwick, 2009): extent is typically continental or global when macroecological processes are being considered (e.g. Araújo and New, 2007), whilst local or regional extents are preferred for studies seeking detailed ecological insight (e.g. Ferrier *et al.,* 2002). Choice of scale is also linked to the generality *versus* specificity dilemma (i.e. whether the model is being developed specifically to describe the habitat associations of the focal population or for predictive application to other populations or areas). For a full consideration of this, see Van Horne (2002). The number of variables is also important to the generality *versus* applicability dilemma (see Section 1.4.5 and Burnham and Anderson (2002) for more information). Local extent and fine resolutions are generally better for investigating the responses of individuals to temporal and spatial resource heterogeneity, whilst broader extents and coarser resolutions are typically better suited to assessing population distribution along broader environmental gradients and revealing likely range shifts over larger geographical areas (Wiens, 2002; Guisan and Thuiller, 2005).

Some researchers have demonstrated the utility of assessing species-habitat relationships at multiple scales (e.g. Mackey and Lindenmayer, 2001; Whittingham *et al.,* 2005; Qi *et al.,* 2012), in a hierarchical fashion; typically these studies investigate the effects of climate determining distribution at a global or national scale (largest extent, coarsest grain), whilst at scales of a few to hundreds of kilometres, topography and substrate type are given greater attention (e.g. Mackey and Lindenmayer, 2001). At the finest scale (smallest extent, finest grain), unique habitat features are often quantified at scales of tens to hundreds to meters (e.g. Whittingham *et al.,* 2005). It is possible to incorporate this hierarchical approach into an SDM with explicitly hierarchical structure, with predictors operating at different scales separated into sub-models (e.g. Mackey and Lindenmayer, 2001), whilst Bayesian approaches can incorporate both hierarchical structure and cross-scale processes (Latimer *et al.,* 2006). Other authors have taken a different approach, creating mixed hierarchical regression models allowing nested data structure (Beever *et al.,* 2006), though these require further theoretical and empirical testing to determine whether they perform as well as a well-conceived non-hierarchical model (Elith and Leathwick, 2009).

Where possible, the grain (resolution) of the EGV and species distribution data should match, but may differ due to different scales or methods of collection. In these cases the resolution of the species distribution data typically determines that at which the EGV data are used; EGV data may therefore be aggregated (i.e. averaged to a larger grid cell size) to match the resolution of the species distribution data, and different EGV layers may have to be aggregated or defined at finer resolutions than they were collected in order to achieve consistency across layers. It is also important to consider EGVs and distribution patterns at a matched temporal scale, using data collected from the same time period where possible (van Beest *et al.,* 2012). Combined with data collected at an appropriate spatial scale, this ensures that the species-habitat relationship in a variable, heterogeneous environment is quantified as accurately as possible.

1.4.5 Applying SDMs: The importance of appropriate EGVs

A major criticism of many applications of SDMs is that their formulation all too frequently includes extraneous variables, especially as the measurement, acquisition and integration of these is becoming much easier and cheaper with advances in sensory and GIS technologies, coupled with the widespread use of the internet to find or distribute freely available data. It is becoming increasingly recognised by a number of authors that the inclusion of additional variables simply because they are available and relatively easy to incorporate likely represents bad practice, and many argue for the application of sound ecological knowledge of the focal species in the choice of EGVs, urging the choice of only those variables which are likely to be ecologically relevant (reviewed by Elith and Leathwick, 2009). The inclusion of many variables, the ecological relevance of which has not been fully considered, is open to potentially identifying spurious relationships between species distribution and the environment, or correlations among independent variables. However, it is not simply the inclusion of these variables in initial models that has been criticised but also the procedures used to eliminate extraneous variables from the final model. Often, researchers may include all available data and allow analytical procedures to determine those that are 'important' to describing the species distribution (Stauffer, 2002). For example, multivariate regression models are generally built using variables selected in a stepwise fashion, in a procedure that relies on statistical significance alone for otherwise seemingly 'arbitrary' inclusion of variables in the final model. When such models are being conceived, it is also frequently the case that the order of variable input affects the composition of the final model. Mac Nally (2000: 668) referred to this model selection as 'statistical tinkering', and such stepwise methods are now less frequently used, and more widely criticised (Whittingham *et al.,* 2006). New information theory-based procedures such as Akaike's Information Criterion (AIC; Akaike, 1974; Burnham and Anderson, 2002; Richards, 2008) are thought to encourage greater depth in consideration of the biological significance of potential variables, and evade many of these criticisms. This approach allows variable selection to be based on more sound ecological knowledge of the focal species and their functional relationships with the environment, and allows final model selection to be based on this information theoretic approach, for example using the minimum AIC value, or weighting models based on the AIC value where there is some uncertainty in choosing between the final few model options (Burnham and Anderson, 2002).

Regarding the generality *versus* applicability of the final model, it is generally agreed that fewer (and coarser scaled) variables give greater generality, whilst adding (finer resolution) EGVs will likely provide a model with greater predictive accuracy to the focal population, though the addition of extraneous EGVs, or a decrease in EGV resolution, may lead to different outcomes (Lowe *et al.,* 2010; van Beest *et al.,* 2012). The sampling of resource availability should therefore focus on ecologically relevant EGVs, matched at the appropriate scale.

1.5 Thesis rationale and objectives

This thesis aims to use an integrative ecological niche modelling (local SDM) approach to examine and quantify grey seal (*Halichoerus grypus,* Fabricius) habitat use and preferences at the North Rona (Scotland; 59°06'N, 05°50'W) breeding colony. Typically, SDMs relate species distributions to coarse-scaled EGVs (Engler *et al.,* 2004; Brotons *et al.,* 2004). However, such coarse scales have frequently been criticised, often for providing unclear ecological meaning (Guisan and Thuiller, 2005). As noted above, it is desirable to measure the environment at a scale relevant to the focal species and to the processes of interest. It has previously been noted that the "grey seal breeding system is one in which individual behaviour, habitat selection and ecology operate on similar and measurable scales" (Pomeroy *et al.,* 2005: 554). This allows for the linkage of behavioural and landscape ecology at a functionally relevant scale, something that is not often achieved due to the vastly different scales at which behavioural and landscape ecological variables are typically measured (Lima and Zollner, 1996). The EGVs included were measured at a sub-seal size spatial grain (Chapter 2; Twiss *et al.,* 2001), the scale at which they are likely to directly influence site selection behaviour (Chapter 2); this is important because, at North Rona, coarse-grain quantification of the EGVs would "smooth out" important physical features including barriers to movement (Twiss *et al.,* 2000a). This approach is relatively novel, as few studies have focused on local and high-resolution applications of niche models or SDMs (Seoane *et al.,* 2006; Vanreusel and van Dyck, 2007, van Beest *et al.,* 2012). Using ecologically relevant EGVs likely to be perceived by the focal species allows the SDM to provide practical information about the likely functional processes determining the species' distribution (Guisan and Thuiller, 2005). This is based on good qualitative and quantitative knowledge of the species' life history and likely habitat requirements (Chapter 2). This research is therefore the first to address grey seal habitat preferences using this selection of EGVs simultaneously, as opposed to in a hierarchical fashion, and will also provide the first multi-annual perspective on this issue.

Based on previous research (Sections 2.2 and 2.3), it is hypothesised that female grey seals will show preferences for pupping sites and habitat at intermediate distances to access points from the sea, near to pools of water of low salinity, which are likely to act as sources for 'fresh' drinking water and to provide a means of behavioural thermoregulation to individuals at risk of overheating (Pomeroy *et al.,* 1994, 1999, 2000; Twiss *et al.,* 2000a, 2001, 2002, 2003, 2007; Redman *et al.,* 2001). It is also hypothesised that females will be shown to pup in locations that are less favourable to other females as habitat, which are therefore more favourable to pup survival, and that social effects will have a tangible influence on the distribution of older relative to younger pups, with older pups likely to be found further from adult females than younger pups.

The examination and quantification of grey seal habitat use and preferences will be achieved using ENFA as the integrative modelling approach, alongside an extensive GIS database (see Chapter 2) containing grey seal distribution information and a set of ecologically relevant ecogeographical parameters that have been noted in previous studies to influence grey seal behaviour. These previous studies will be discussed in Chapter 2 as background to grey seal ecology. This thesis will also incorporate, and assess the influence of, new parameters that have been qualitatively assessed as important to grey seal behaviour and physiology (Redman *et al.,* 2001; Twiss *et al.,* 2002). In addition, this data represents a time series spanning 13 years, and will be used to examine both within and between season variation in habitat use and preferences. Within this long-term dataset is information on the distribution of seals of all age classes; this will be utilised to examine variation in habitat use amongst different age classes of the North Rona population, including making a distinction between the pupping site and subsequent habitat preferences of female grey seals, and establishing the effects of potential social interactions on the distribution of pups of various ages. Habitat selection will be assessed by examining the distribution of adult female seals (hereafter simply termed "females", except where this would introduce confusion), whilst pupping site selection will be assessed by examining the distribution of Stage I-II pups (based on the Stages of Boyd *et al.,* 1962), hereafter termed "neonates".

Chapter 2 provides a detailed introduction to grey seal ecology, particularly regarding the grey seal in the UK and at North Rona. General methods are then discussed in Section 2.4. Chapter 3 then provides a quantitative description of the weather and the habitat available at North Rona before exploring general trends in seal distribution and habitat associations. These quantitative assessments are made at several points in time during each of five breeding seasons as the habitat, particularly pool distribution, is known to change over time, with the colony generally becoming wetter with more standing water later in the season (P.P. Pomeroy (PPP) and S.D. Twiss (SDT), *pers. comm.*) and these changes may influence site selection. In Chapter 4 the habitat associations of adult female grey seals are explored in further detail using ENFA to examine the influence of the quantified EGVs on seal distribution. This chapter will also investigate differences between pupping site selection and subsequent habitat use of female grey seals. In Chapter 5, discriminant analysis (Legendre and Legendre, 1998) is applied in order to assess the differences in resource use (the 'niche separation') between young, dependent pups (Stage I-II pups; 'neonates') and older, weaned pups (Stage V pups; 'weaners') to determine how their distribution is affected by both environmental and social variables. Finally Chapter 6 discusses the broader implications of the results and provides suggestions for future research.

2. Methodology

2.1 Introduction

This chapter provides an introduction to the study species for this research, the grey seal, including relevant background information on breeding ecology. Specifically, it will explore the ecology of the grey seal in the United Kingdom and North Rona, the field site for this research. Following a general introduction to the study system and site, general methods will be discussed in this chapter to avoid repetition in later chapters; however, methods specific to particular chapters and specific details of analytical methods will be explored in subsequent relevant chapters.

2.2 The grey seal

The grey seal is a large phocid first described by Fabricius (1791) and given its current Latin binominal by Nilsson (1820). This section provides an introduction to its distribution, taxonomy and appearance (Section 2.2.1) in addition to behaviour, ecology and habitat associations (Section 2.2.2).

2.2.1 Distribution, taxonomy and physical description

The grey seal is found only in the Northern Hemisphere, in the temperate and sub-arctic waters of the eastern (Hewer, 1960; SCOS, 2011) and western (Boness and James, 1979; NOAA, 2011) North Atlantic coastlines, with an additional, isolated population in the Baltic Sea (Harding *et al.,* 2007; Jüssi *et al.,* 2008). There are thought to be approximately 300,000 individuals worldwide, 38% of which comprise the UK subpopulation (111,300 at the start of the 2010 breeding season; SCOS, 2011). The majority (88%) of the UK population can be found in Scotland, with an estimated UK-wide annual pup production of over 50,000 (SCOS, 2011). The majority of the remaining seals can be found in the east Atlantic, as the Baltic Sea population numbers only a few thousand, though is steadily expanding (Harding *et al.,* 2007). Recently confirmed sightings also place grey seals living in grottoes (small caves liable to inundation with water at high tide) of the Black Sea and it is thought likely that these individuals have been introduced from the coastal aquariums of Ukraine and Russia (Kovtun, 2011). Very little is known about these individuals or whether the population is large enough to be sustainable.

There are currently 19 recognised species and 16 subspecies of phocid (Berta and Churchill, 2012) and the grey seal is represented by two subspecies; the Atlantic grey seal *Halichoerus grypus grypus* (Fabricius, 1791) and the Baltic grey seal *H.grypus macrorhynchus* (Hornschuch and Schilling, 1851). However, a brief review of the history of the classification of the grey seal reveals some debate as to its taxonomy. Behavioural and physiological differences

between the eastern Atlantic and western Atlantic stocks of *H. grypus grypus* suggest that these stocks should be classified as distinct subspecies, supporting Nehring's (1886) identification of three distinct 'varieties' of grey seal (eastern North Atlantic, western North Atlantic and Baltic). Following the identification of differences in cranial morphology between the stocks (Chapskii, 1975), the three varieties were indeed classified as distinct subspecies. However, the eastern and western Atlantic stocks were subsequently reclassified as the same subspecies (Heptner *et al.,*1976) despite molecular studies supporting Nehring's proposition: Boskovic *et al.* (1996) found distinct differences in mitochondrial DNA between the three stocks. Current taxonomic classification still recognises only two distinct subspecies (Berta and Churchill, 2012). The research presented in this thesis is focused on a breeding colony from the eastern North Atlantic stock of *H. grypus grypus;* therefore the background material presented here will focus mainly on this stock. This seems an appropriate approach given the focus of this research and the behavioural and physiological differences between grey seal populations and subspecies (Boness and James, 1979; Fedak and Anderson, 1982; Anderson and Harwood, 1985; Anderson and Fedak, 1987a,b; Bowen *et al.,* 1992; Iverson *et al.*, 1993). For more detail on the western Atlantic population of *H. grypus grypus,* see Boness and James (1979) and NOAA (2011), or Harding *et al.* (2007) and Jüssi *et al.* (2008) for information on the Baltic populations of *H. grypus macrorhynchus*.

The grey seal is one of the most sexually dimorphic phocids, second only to the genus *Mirounga.* Males can weigh 170-310kg and reach 2.3m long, whilst females are typically 1.6-2m long and, on North Rona, weigh an average of 190 ± 23 (SD) kg post-partum (Pomeroy *et al.,* 1999). Both sexes are typically smaller and lighter than their western North Atlantic counterparts (Anderson and Fedak, 1987a; Bowen *et al.,* 1992; Iverson *et al.,* 1993). In addition to body size differences, there are a number of morphological differences between the sexes; for example, males typically have heavier chests and necks, and much larger snouts, which are thought to act as a display structure similar to that of the hooded seal, *Cystophora cristata*, and the northern and southern elephant seals, *Mirounga angustrorostris* and *Mirounga leonina* (Miller and Boness, 1979). The pelage of the adult grey seal is typically grey but may vary between grey, brown and black, and males are generally darker than females; it is possible to identify individuals of both sexes by the pattern of dark blotches on the pelage (Vincent *et al.,* 2001; Hiby *et al.,* 2012) or, particularly in males, by scarring patterns (Twiss *et al.,* 1998, 2006). This is useful for long-term repeat studies on groups of 'known' individuals (for example, Pomeroy *et al.,* 2000b; Twiss *et al.,* 2011), as individuals may be tracked within and between seasons without the need for tagging or branding, providing a hands-off, zero-disturbance approach to individual identification.

2.2.2 Behaviour, ecology and habitat associations

The grey seal is a colonially breeding species and, in the UK, tend to form breeding colonies on uninhabited beaches or remote islands which are largely undisturbed by humans. Individual colonies typically form for eight to ten weeks in the autumn and winter (Coulson and Hickling, 1964; Anderson *et al.,* 1975). The specific dates of colony formation vary according to location but are relatively consistent for a specific site as individuals generally return to their natal breeding colony within a few days of their pupping date in the previous year (Pomeroy *et al.,* 1999). Indeed, both females and males show remarkable fidelity to previous breeding sites (Pomeroy *et al.,* 1994; Twiss *et al.,* 1994), as indicated by resightings (Pomeroy *et al.,* 2000b) and differences in microsatellite allele frequencies between colonies (Allen *et al.,* 1995). Not only do individuals tend to return to the same colony, but females will return to sites closer to previous pupping sites within a colony than could be expected by chance (Pomeroy *et al.,* 2000b). For example, females on North Rona return to sites within a median distance of 55m from the previous years' pupping site (Pomeroy *et al.,* 1994; Pomeroy *et al.,* 2000b), whilst males show similar fidelity to their previous breeding site (median distance of 53m; Twiss *et al.,* 1994). This is especially remarkable given the often large ranges of individuals outside of the breeding season: individuals captured and satellite-tagged on the east coast of the UK travelled to locations up to 2100km away (McConnell *et al.,* 1999). The earliest colonies to breed are in the south-west of England, Wales and Ireland, which form in early September each year, with subsequent colonies pupping in a clockwise pattern around the UK (SCOS, 2011). Colonies in the north of Scotland (such as North Rona and the Isle of May, Firth of Forth (56° 11′ N, 02° 33′ W)) form towards the end of September whilst those in the east of England (such as Donna Nook, Lincolnshire; 53° 28' N 00° 09' E) do not form until the end of October and breeding seals may be present until early January. During the breeding season, an individual breeding female will stay ashore for an average of 18-20 days. There is thus a turnover of females throughout the season as individuals will not stay ashore for the entire colony breeding period.

Upon arrival at the breeding colony, pregnant females spend an average of four days ashore before parturition (Pomeroy *et al.,* 1999). It is thought that this time is spent in site selection before the females give birth to a single pup (Hewer, 1960; Burton *et al.,* 1975; SCOS, 2011). The site choice exhibited in this time is thought to be based largely on the females' requirement for proximity to water; females typically preferentially colonise areas close to pools of water or near to access points from the sea (Boyd *et al.,* 1962; Anderson *et al.,* 1975; Pomeroy *et al.,* 1994; Twiss *et al.*, 2000a), though not immediately next to access points, which are implicated in increased pup mortality (Twiss *et al.,* 2003).This requirement for proximity to water is largely due to thermoregulatory requirements (Redman *et al.,* 2001), but may also be important in the maintenance of a positive water balance during the breeding fast; indeed, many

investigators have witnessed individuals drinking from pools of water (Twiss *et al.*, 2000a, 2001, 2002; Redman *et al.,* 2001). During their time on the colony, post-partum females do not return to the sea to feed but obtain their energy by metabolism of stored reserves including lipids in their thick blubber layer (Pomeroy *et al.,* 1999). These reserves are also mobilised to provision the pup with a lipid-rich milk which may contain anywhere from 30% to 60% lipids; the variation in this amount is accounted for by individual differences in maternal condition and the age of the pup (Lydersen *et al.,* 1995; Pomeroy *et al.,* 1999; Debier *et al.,* 2003). As a result females lose on average 82kg during their time on the colony, which is equivalent to an average loss of 46.5% of their body mass (Pomeroy *et al.,* 1999) and is transferred to the pup with an efficiency of approximately 45% (Pomeroy *et al.,* 1999) on North Rona. Pups grow from a mean birth mass of 16.5kg to an average weight at weaning of over 40kg, with an average mass gain of 1.7kg day^{-1} over an average of 18 days (Pomeroy *et al.,* 1999). This is comparable to the maternal mass transfer efficiencies seen at other sites (e.g. Sable Island, Nova Scotia, 43° 56′ N 59° 55′ W; Iverson *et al.,* 1993) and in other pinnipeds (e.g. southern elephant seals; Fedak *et al.,* 1996), and is also comparable to that recorded previously for grey seals at North Rona (46.1%; Fedak and Anderson, 1982).

During lactation the female will generally remain in close proximity to her pup, either on land or close to the shore (Twiss *et al.,* 2000a), though this varies depending on the local topography of the breeding colony. On North Rona females generally remain on land due to the high cost of locomotion between their pupping site and the sea, which may be as far as 200m (SDT, *pers. comm.*). Conversely, females on the open sandy beaches of the Monach Isles (Outer Hebrides, Scotland; 57° 48′ N, 7° 15′ W) spend three times as long as North Rona females in locomotion between their pup and the sea, a distance which is rarely greater than 50m (Anderson and Harwood, 1985). Females on North Rona therefore remain on land at an average distance of approximately 2.75 ±0.2 (SD) m from their pup (SDT, *pers. comm.*), with median daily movements, for example to nearby pools of water, typically occurring within 10m of the pup (PPP, *unpubl. data;* Redman *et al.,* 2001). On approximately day 16 of lactation the female will enter oestrus (Pomeroy *et al.,* 1999; Twiss *et al.,* 2006) and may mate with one or more males before returning to the sea (Twiss, 1991; Twiss *et al.,* 2006). Males typically become socially mature at eight years of age and have reproductive lifespans of up to 15 years. This is substantially shorter than the reproductive lifespan of females, which mature at three to five years of age and may breed for over 25 years, up to 42 years of age (Hewer, 1960; Pomeroy *et al.,* 1999; Worthington Wilmer *et al.,* 1999; Bowen *et al.,* 2006). The pup is abruptly weaned when the female returns to the sea, normally 18 days post-partum (Hewer, 1960; Fogden, 1971). Rather than immediately going to sea, weaned pups will generally move to the outskirts of the colony to areas of lower adult density (Coulson and Hickling, 1964; Hewer, 1974; Twiss *et al.,* 2001) where they remain for

several weeks before entering the sea (Fedak and Anderson, 1982), meeting their energy requirements through the metabolism of stored lipids in their blubber layer (Coulson and Hickling, 1964; Bennett *et al.,* 2007). Given the high degree of maternal investment in pups, it seems counter-intuitive that pups should subsequently fast before going to sea, and the reasons for the post-weaning fast are unclear, though are discussed in detail in Chapter 5 (Section 5.1).

2.3 The field site

This section will introduce the field site, North Rona, an important breeding colony for Eastern Atlantic grey seals (Section 2.3.1), before briefly outlining the status of the grey seal at North Rona, and the importance of North Rona to ecological research (Section 2.3.2). The specific study site for the research reported here is also defined (Section 2.3.3).

2.3.1 North Rona

North Rona (Figure 2.1 and 2.2) is a small island located 75.5km NNW off Cape Wrath, Scotland, which has been designated as a Special Area of Conservation (SAC) under the Habitats Directive (EC Directive 92/43/EEC) since March 2005. This designation is based partly on the presence of a population of grey seals on the island, which at the time represented the third largest UK breeding colony, though has since declined (Duck and Morris, 2011). The island covers an area of approximately 1.2km^2 and rises to a maximum of 108m above sea level, with some cliffs reaching to 75m above sea level (Pomeroy *et al.,* 1994). Due to the locations of cliffs, which surround most of the island, and lack of beaches, there is limited access to the island from the sea; the main access points to the major seal breeding area on North Rona are a series of gullies (Anderson and Harwood, 1985) on the east side of the low-lying Fianuis peninsula (Figure 2.3). Fianuis peninsula covers an area of approximately 1.0 × 0.3km and has been sub-divided into four distinct geographical areas by previous researchers on North Rona (Figure 2.2; for example, Pomeroy *et al.,* 1994; Twiss *et al.,* 1994; Poland *et al.,* 2008) on the basis of topographical features, including the gullies indicated in Figure 2.3, and divisions in the general distribution of seals. These four areas are, from north to south, known as Fianuis North (FN), Fianuis Central (FC), Fianuis South (FS) and Study Area (SA). The topography of North Rona is mostly composed of undulating grassy terrain punctuated by irregularly spaced fresh to brackish water pools of variable size, boulders and the remains of stone walls created by previous inhabitants (though the island has not had permanent inhabitants since 1885; Darling, 1952).

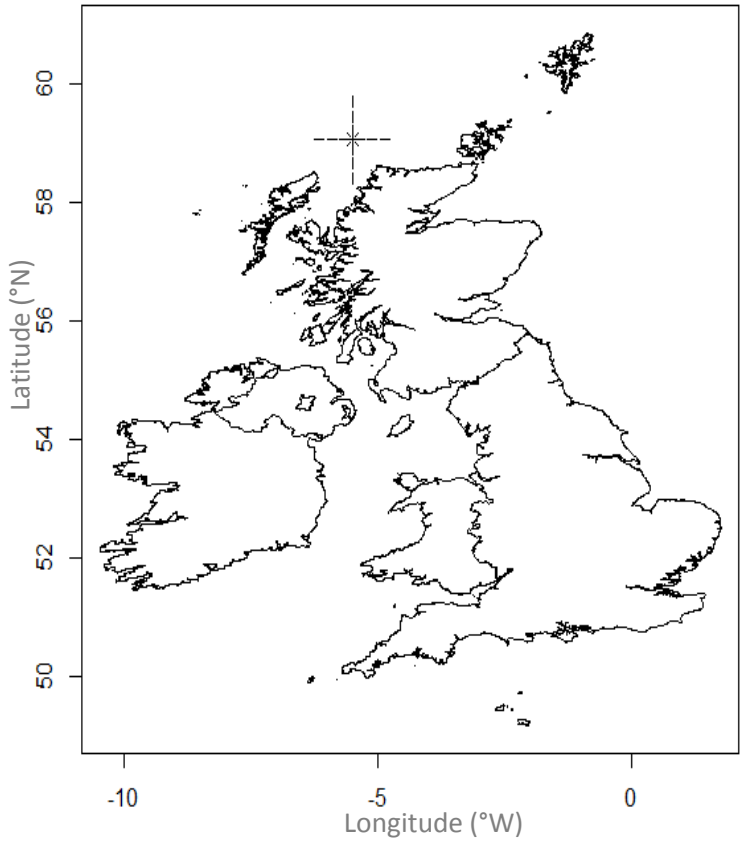


Figure 2.1: The position of North Rona in relation to the rest of the United Kingdom. The crosshairs (⌖) at 59°06'N, 05°50'W indicate the location of North Rona. Adapted from a shapefile of the UK and Ireland coastline available from http://og.decc.gov.uk.

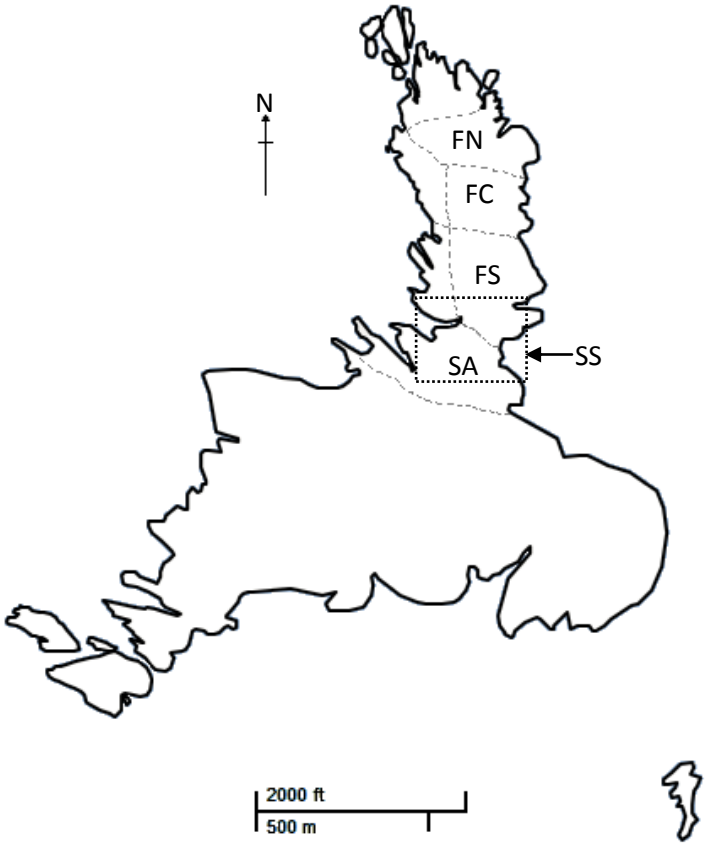


Figure 2.2: Map of North Rona indicating divisions of the Fianuis peninsula; SA = 'Study Area', FS = 'Fianuis South', FC = 'Fianuis Central', FN = 'Fianuis North'; SS = 'Study Site' (region bounded by dotted box, encompassing part of SA and the south of FS; see Section 2.3.3 and Figure 2.3). Adapted from outline view of North Rona from Google Maps ©2012 Google.

2.3.2 The grey seal at North Rona

North Rona has hosted ecological research focused on the breeding colony of grey seals since the late 1950's (for example, Hewer, 1960; Boyd and Laws, 1962; Boyd *et al.,* 1962; Boyd and Campbell, 1971), though the colony is thought to have become established at some time between 1844 and 1880 (Harvie-Brown and Buckley, 1888; Pomeroy *et al.,* 1994). In more recent years, studies focused predominantly on the Study Area and performed at an increasingly fine spatial scale have addressed a number of important ecological issues, including: the determinants and effects of distribution and site use and fidelity (Pomeroy *et al.,* 1994, 2000b, 2005; Twiss *et al.,* 1994), causes of individual variation in reproductive success (Twiss *et al.,* 1998; Pomeroy *et al.,* 1999), colonisation patterns (Twiss *et al.*, 2000a; 2001), importance of topography at a fine spatial scale within the colony (Twiss *et al.*, 2000a; 2001, 2002; Redman *et al.,* 2001), relatedness and paternity (Pomeroy *et al.,* 2000b; Twiss *et al.,* 2006; Poland *et al.,* 2008), the influence of climate on seal distribution, maternal attendance and degree of polygamy (Redman *et al.,* 2001; Twiss *et al.,* 2002, 2007), determinants of pup mortality (Twiss *et al.,* 2003), extent of sociality (Pomeroy *et al.,* 2005; Ruddell *et al.,* 2007), degree of sexual selection (Twiss *et al.,* 2007) and consistent individual differences in behaviour (Twiss and Franklin, 2010; Twiss *et al.,* 2011, 2012; Culloch, 2012). These studies have progressed towards an assessment of the ecology of individuals within the colony rather than the population as a whole, as was previously common at North Rona (e.g. Boyd and Laws, 1962; Boyd and Campbell, 1971).

The North Rona grey seal breeding colony contributes 5% of annual UK pup production (though this figure is declining; Duck and Morris, 2011), and is concentrated on Fianuis peninsula. There is some inter-annual variation in the number of pups born in each area of the Fianuis peninsula (Boyd and Campbell, 1971; Anderson *et al.,* 1975; Summers *et al.,* 1975), but overall 95% of the colony's pups are born on the peninsula each year (Boyd and Laws, 1962; Boyd *et al.,* 1962) and females generally show a high degree of pupping site fidelity (Pomeroy *et al.,* 1994). Though the breeding season on North Rona stretches from late September to late November (Boyd and Laws, 1962), the majority (*c.* 95%) of pups are born in a six-week period between 19th September and 29th October (Harwood *et al.,* 1991; Hiby *et al.,* 1996), with a peak in pup production generally occurring around the 8th October each year (Pomeroy *et al.,* 2000b). There is an overall seasonal pup mortality rate of approximately 14.5%, as determined by multiple studies over a number of decades (Boyd and Laws, 1962; Boyd and Campbell, 1971; Twiss *et al.,* 2003). Pup production was relatively stable between 1995-2000 following a period of increase (Hiby *et al.,* 1996; Pomeroy *et al.,* 2000b) but has been in decline in the last decade (Smout *et al.,* 2009; Duck and Morris, 2011; C.D. Duck (CDD) and PPP, *unpubl. data*).

2.3.3 The study site

Most research in the past two decades (outlined above) has focused on SA, with some recent work also occurring in FN/FC (Culloch, 2012); however, the research presented in this thesis is focused on a 287m × 287m area encompassing the majority of SA and the south of FS, as shown in Figure 2.2 ('Study Site'; SS) and in more detail in Figure 2.3.

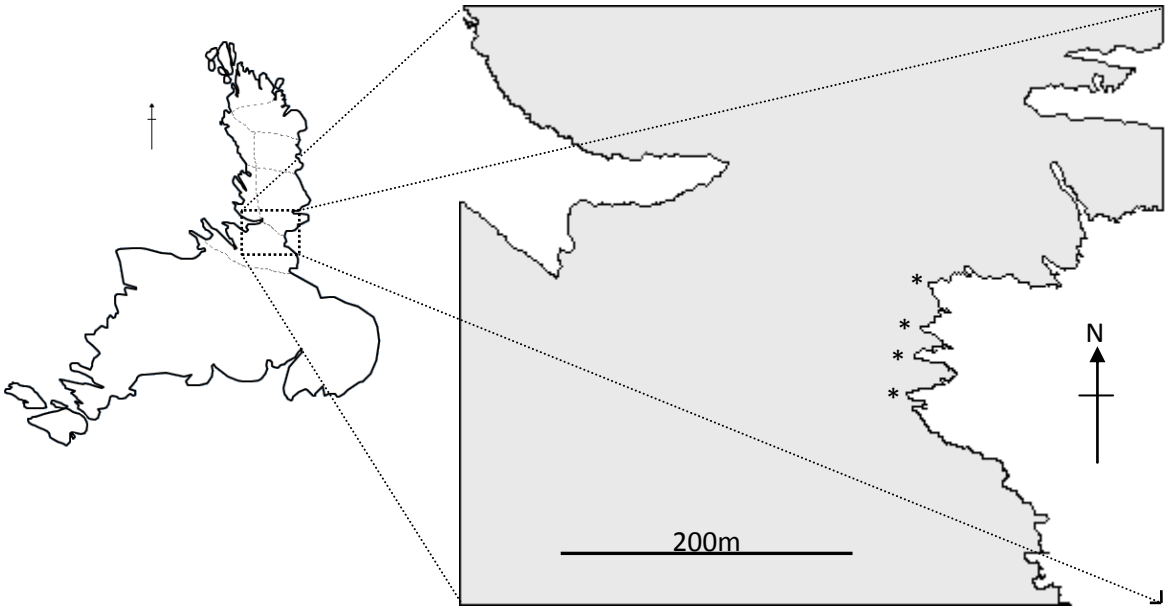


Figure 2.3: Outline of the SS for the research presented in this thesis in relation to the rest of North Rona. See Figure 2.2 for details of previously defined areas. Asterisks (*; placed on-land) indicate the location of the main access gullies to and from the sea. Areas of land shaded grey.

2.4 Data collection and analyses

The data presented in this thesis may be broadly classified as i) seal location data ii) EGV data and iii) weather data. The seal location data (Section 2.4.2) includes fine-scale daily locations of all seals within the SS on the fieldwork dates outlined in Section 2.4.2. EGV data (Section 2.4.3) were derived from multiple sources, including a Digital Terrain Model (DTM; Section 2.4.3.1), aerial photography from aerial surveys conducted by the Sea Mammal Research Unit (SMRU) for the annual grey seal population census (Sections 2.4.1 and 2.4.3.2) and in-field sampling (Section 2.4.3.3). The weather data were also collected from various sources (Section 2.4.6). The majority of this work was carried out using an extensive geo-referenced database of spatial information created, stored and manipulated in the software ArcInfo (Versions 7.0.3-9.3; Environmental Systems Research Institute Inc. (ESRI), 380 New York Street, Redlands, California, USA).

For all EGVs and individual locations, only data within the SS boundaries (Figure 2.3), were entered into the GIS database and included in analyses. The boundaries of the SS were formed by a square defined by the Ordnance Survey (Great Britain; OS GB) coordinates:

- X-Minimum = 181150
- X-Maximum = 181530
- Y-Minimum = 1032600
- Y-Maximum = 1032900

2.4.1 Aerial photography

During the grey seal breeding season, SMRU conduct pupping censuses using high-resolution aerial photography surveys of a number of colonies in Scotland (Hiby *et al.,* 1988; Duck *et al.,* 2003). These aerial surveys are performed using a Linhof Aerotechnika (5 x 4 inch format) camera fitted with a 150mm lens. Photographs are taken at an altitude of approximately 366m (Twiss *et al.*, 2000b). Several surveys are taken of each colony, including North Rona, throughout each breeding season, providing images of each colony at several time points. Courtesy of C.D.D. (SMRU), aerial photographs were made available for the SS during each of the five focal breeding seasons (Section 2.4.2). Aerial photographs were available for an average of three time points in each season, generally 7-14 days apart, and a selection of 4-5 photographs is typically sufficient to cover the SS for each "stage" of the breeding season. Breeding season stages are defined in Section 2.4.2 (Table 2.1). Photographs from the 1994 breeding season were used in the construction of a Digital Terrain Model (DTM) of North Rona (Section 2.4.1 and 2.4.3.1; Twiss *et al.,* 2000b) and to establish the GIS database used throughout this research. Aerial photographs used in construction of the DTM (Section 2.4.1) were collected in a series of aerial surveys performed on five dates in 1994: 27th September; 8th, 21st and 31st October; and 16th November (Twiss *et al.,* 2000b). Following collection, the aerial photographs from 1994 were scanned on to Kodak Photo-CD at a resolution of 4096 × 6144 pixels and then transferred to the GIS as TIFF images (Mills *et al.,* 1997).

Aerial photographs taken in 1994 were "ground-truthed" using Global Positioning System (GPS) ground control points (GCPs) identifiable in the images and located in the field post-breeding season by a metre-accurate carrier phase differential GPS (Magellan Nav 5000 Pro; Twiss *et al.,* 2000b). GCPs allowed georectification of the 1994 aerial photographs to real-world OS GB coordinates. Key features of the SS identified in the georectified aerial photographs were digitised as line features within an ArcInfo GIS coverage; these features included the coastline, large rocks, permanent hollows and stone walls. Later aerial photographs (Section 2.4.3.2) were then georectified to this coverage by matching key features throughout the SS identified in the photographs to identical features in the coverage. Aerial photographs from 1994 were also used to create a base map of the SS, as OS GB maps were not available at a satisfactorily fine resolution. This base map (Figure 2.5) incorporated detailed habitat features, such as those used to georectify the aerial photographs, and a 10m × 10m grid overlay to enhance precision in fine-scale mapping of individual grey seals (Section 2.4.2).

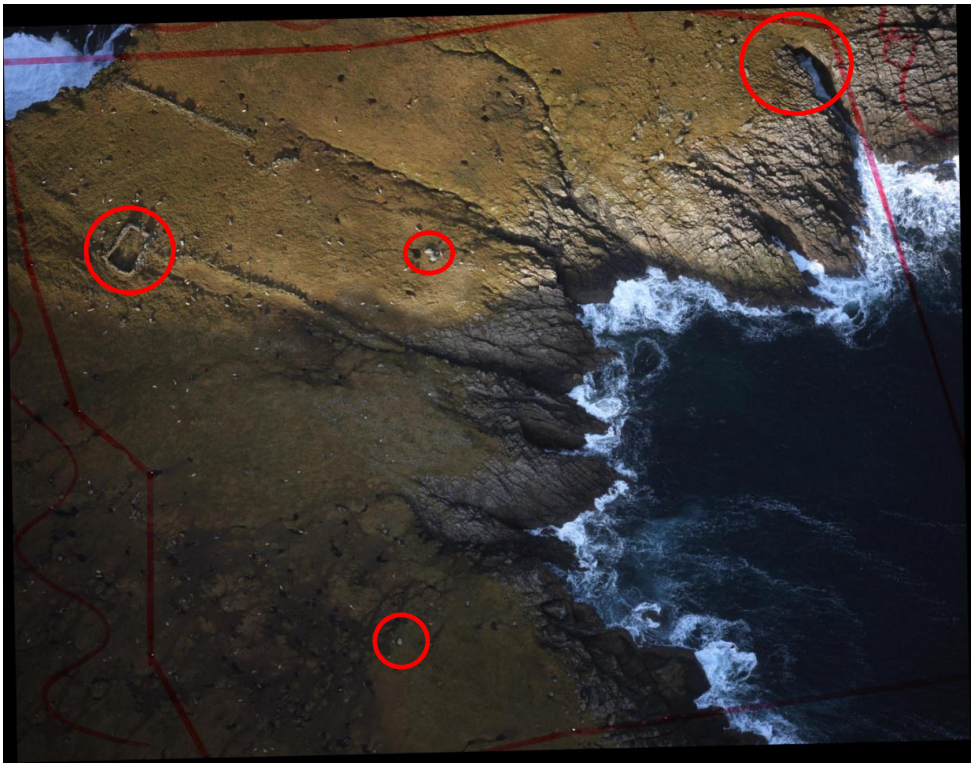


Figure 2.4: Example of an aerial photograph taken by SMRU for the annual pupping census. This photograph shows the main part of the SS, including several key features useful for georectifying the aerial photograph to real-world OS GB coordinates (circled in red).

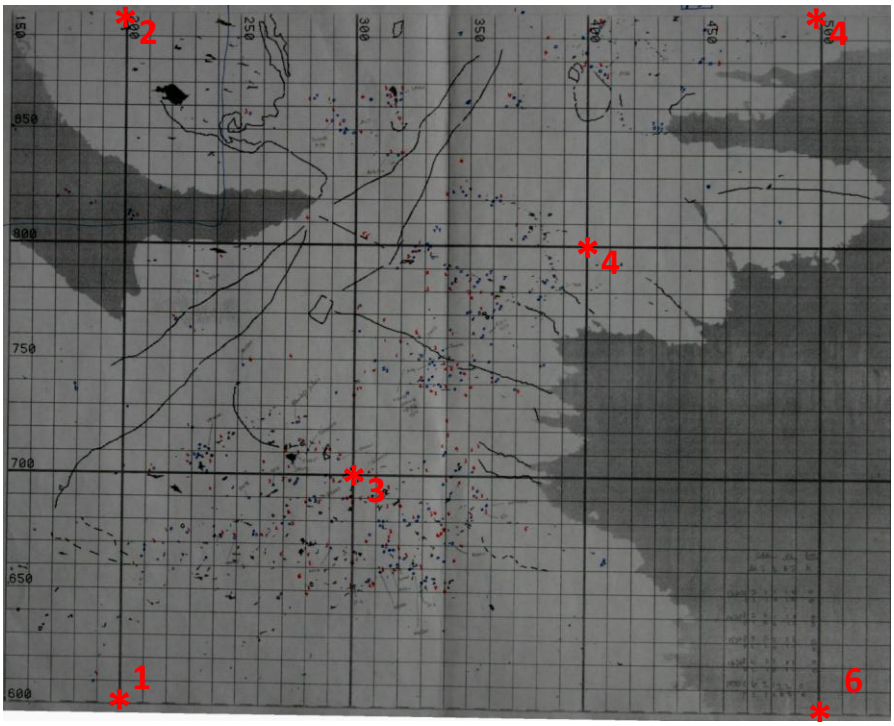


Figure 2.5: Example of a fine-grain SS base map used for recording daily locations of individual grey seals. Base map includes detail of key topographic features such as land extent, gullies, large rocks and stone walls for reference, in addition to a 10m × 10m grid overlay. "Tics" used for map georectification (Section 2.4.2) are indicated by red asterisks; OS GB coordinates: Tic 1: (181200, 1032600); Tic 2: (181200, 1032900); Tic 3: (181300, 1032700); Tic 4: (181400, 1032800); Tic 5: (181500, 1032900); Tic 6: (181500, 1032600).

2.4.2 Seal location data

Spatial location data for all individuals (adult males, adult females and pups) was collected in-field by PPP and SDT from observation blinds at the top of a slope overlooking the SS from the south on all dates indicated in Table 2.1. All location data were recorded with sub-metre accuracy on fine-grain base maps of the SS (Figure 2.5; Section 2.4.1), using the head of each individual as a standard mapping reference point. Sub-metre accuracy was achieved using key landmarks identifiable on base maps and in-field as reference points (Pomeroy *et al.,* 1994). To maintain accuracy in relative positions of individuals, the mapping process was performed as quickly as possible. The resulting maps were digitally transferred to a PC via digital photography, performed with a Canon EOS 3OD camera (28-135mm Canon EF lens) from a height of approximately 1m using a tripod, flash and remote shutter release to avoid blurring. Digital images of the maps were then georectified to real-world OS GB coordinates within an ArcInfo GIS using six points (tics), defined by the grid overlay, which represent the intersections of the main eastings and northings.

These geo-rectified images were then used as backdrops within ArcInfo to digitise all individuals into daily point coverages. Each individual location within the GIS was thus associated with a real-world OS GB coordinate in addition to the data collection date and information on the sex and age class of the seal (adult male, adult female or pup), including categorisation of pup age classes "I" to "V" (as defined by Boyd *et al.,* 1962) or as dead pups. Individual female identities were also included, as determined by pelage markings (Pomeroy *et al.,* 2000b; Vincent *et al.,* 2001 Twiss *et al.,* 2011; Hiby *et al.,* 2012), brands and flipper tags (Pomeroy *et al*., 1994; Redman *et al.,* 2001). Pup GIS coverages were initially created which contained the locations of all pups (Stages I through V). New daily coverages (neonates only and weaners only) were created in ArcInfo using the additional information on pup stage stored within the GIS to select only Stage I and II pups or only Stage V pups.

Adult female and neonate locations on all dates (Table 2.1, "Dates Collected") were used to describe the daily trends in female and neonate numbers on the colony (Section 3.3.3), but for niche modelling, specific dates were chosen to represent the early, middle and late stages of the breeding season, partly to avoid pseudo-replication as female and pup distribution changes little on a daily basis. The dates chosen were used as these are the dates for which pool distribution data were available (Section 2.4.3.2). These categorisations were carried out primarily for ease of reference to a particular set of aerial photographs and model iterations (e.g. photographs from "Late 2008" rather than from "29th October 2008"). This also allows for a comparison of each "Stage" between years, and for assignation of salinity data to the appropriate pool data (Section 2.4.3.3); however, the scope for direct comparison is limited as each Stage did not correspond to the same date in each season (Table 2.1). Days on which both seal and pool distribution data were analysed will hereafter be referred to as "focal days".

Table 2.1: Summary of seal survey dates and the breeding season "stage" that these were associated with.

Year	Dates collected	Dates analysed† (DD/MM)	Corresponding stage of breeding season
1998	29/09 – 27/10	10/10	Early
		17/10	Mid
		25/10	Late
2004	29/09 – 04/11	03/10	Early
		16/10	Mid
		26/10	Late
2008	28/09 – 01/11	05/10	Early
		17/10	Mid
		29/10	Late
2009	28/09 – 02/11	24/10	Late
		02/11	End
2010	28/09 – 03/11	30/09	Beginning
		12/10	Mid
		24/10	Late
		03/11	End

†This refers to the dates analysed in statistical analyses and in SDMs in this thesis (focal days). However, in Section 3.3.3, all dates are analysed in order to describe the trend in female and neonate numbers on the colony throughout each breeding season.

2.4.3 Ecogeographical variable data

2.4.3.1 Digital Terrain Modelling and 'cost-distance' surfaces

Much of the EGV data were derived, at least in part, from a sub-meter accurate DTM of the SS, which provides accurate descriptions of elevation above mean sea level (m) and slope (degrees). The DTM was created using georectified aerial photographs of the SS (Section 2.4.1). From these photographs, a DTM was generated with a grid cell resolution of 0.2m × 0.2m. For full details of this process, see Mills *et al.* (1997) and Twiss *et al.* (2000b).

The elevation and slope values provided by the DTM were used to derive the following three EGVs for use in this study: (i) 'cost distance' to 'nearest' access point from the sea (CACC); (ii) 'cost distance' to 'nearest' pool of water (CPOOL; Section 2.4.3.2); (iii) 'cost distance' to 'nearest' female (CFEM; Chapter 5). These variables were chosen as they appear to be relevant to grey seal ecology, as outlined in Section 2.2; previous research has suggested that females may prefer sites at intermediate distances to access points to the sea, possibly because sites too close to access risk disturbance from seals leaving or arriving to the colony, whilst sites too far from access may be avoided due to the higher cost of locomotion required to reach them (Pomeroy *et al.,* 1994; Twiss *et al.,* 2000a; Twiss *et al.,* 2003; Stephenson *et al.,* 2007). Proximity to temporary pools of water, which form as a result of rainfall and sea spray, is likely to be preferred by adult females as these pools aid thermoregulation by individuals experiencing thermal stress and may also provide drinking water to assist in the maintenance of a positive water balance (Redman *et al.,* 2001; Twiss *et al.,* 2002). Stephenson *et al.* (2007) suggested a role for aggression in female site choice, and the CFEM variable was derived as an individual is likely to experience greater

aggression when near to other females than when far from neighbouring females; this CFEM variable can therefore be interpreted as probability of aggression, with lower 'cost' suggesting a higher probability of aggression. The CFEM variable only becomes relevant in Chapter 5, though both CACC and CPOOL are used extensively throughout this research. These 'cost distance' variables provide an index for each location in the SS of the relative ease of movement between that location and the 'nearest' feature of interest (pool, access point or female neighbour). However, rather than just measuring absolute straight-line distance between these points, the 'nearest' point is defined as that which is easiest to get to in terms of accumulative cost of movement over the uneven terrain of the SS. Note that this does not imply knowledge of the energetic cost incurred by the seals but that 'cost' is simply a function of the slope traversed in moving between grid cells and the surface distance travelled. Each 'cost-distance' variable is calculated to provide the lowest accumulative 'cost' between a focal position and the feature of interest. Incorporated into this, therefore, is information on the elevation and slope of the SS, in addition to insurmountable obstacles which require a detour to pass (for example, vertical cliff faces). Intuitively, this representation of seal movement should give a slight advantage to movement down slopes, with greater cost for uphill movement and include barriers to locomotion dependent on the movement capabilities of seals. Adult grey seals are approximately 2m long and are capable of climbing near-vertical faces provided their fore-flippers can reach the target location (SDT, *pers. comm.*); near-vertical faces of 2m or greater were therefore assumed to be barriers to any movement and required that a path around the obstacle be taken.

The 'cost distance' surfaces were created using the ARC-Info command PATHDISTANCE, which factors in the surface distance traversed in addition to vertical factor modifications which influence the cost of moving between locations based on the elevation and slope values in the DTM. The vertical factor was calculated as the square of the cosine function of all negative (downhill) slopes and the square of the secant function for all positive (uphill) slopes encountered, following Twiss *et al.* (2000a). This ensures that small upward slopes present small costs, whilst cost increases as the angle of the slope climbed increases; it also ensures that, similarly, there is little change in cost for descending shallow slopes, but a greater decrease in cost as the slope gets steeper, To include barriers to movement in the surface, where the slope between two grid cell centres exceeded 78.69^{o} (positive or negative) the vertical factor was set to infinity. A slope exceeding this value between consecutive cells represents a change in elevation of 2m or greater and therefore presented insurmountable barriers to locomotion between cells.

The slope, elevation and features such as the coastline and stone walls of North Rona were assumed not change within or between years, as these represent permanent features of the local topography (PPP and SDT, *pers. comm.*). Therefore, a 'cost' surface was created once for access points (CACC) using the above methodology and a grid depicting the access points as an

input grid (grid cell size = 0.2m × 0.2m). In addition a grid with 1m × 1m grid cell resolution was created depicting the elevation profile of the SS (ELEV), with elevation values derived from the SS DTM. The only topographical feature which could potentially change within and between years is the number, extent and distribution of temporary pools of water (PPP and SDT, *pers. comm.*). Creation of cost surfaces for pools (CPOOL) is described in Section 2.4.3.2. The creation of the CFEM surface is described in Section 5.2.1.2.

2.4.3.2 Pool distribution

Aerial photographs of the SS spanning multiple years were selected from the aerial photography archive (Table 2.2). An average of three sets of aerial photographs were taken of the SS each year; these sets were grouped according to approximately when in the breeding season they were taken: the beginning, early, middle, late and end of the season (Table 2.2). Each SS photograph was individually electronically scanned into the computer database at a resolution of 2400dpi. The photographs were then georectified to real-world coordinates within the GIS. The coverage used for geo-rectification had been created previously using georectified aerial photographs from the 1994 breeding season (Section 2.4.1). For each focal day, the SS was represented by a collection of three or four slightly overlapping photographs.

Pools were digitised as polygon coverages in ArcInfo, using georectified digital copies of the aerial photographs as backdrops. Due to variable lighting conditions (intensity, direction and angle of sunlight), it was occasionally difficult to distinguish between pools of water, dry hollows and muddy wallows. Therefore, during digitisation of all possible pools, polygons were labelled (based on judgements made by J.E. Stewart (JES) at a consistent zoom level for the purpose of reliability) with decreasing certainty from 1-3 according to the certainty with which it could be claimed to represent a pool. Following a review of all polygons, all subsequent analyses used only category 1 polygons, to avoid introducing increased uncertainty to the interpretation of results. Individual pool coverages, each representing a section of the SS, were merged in ArcInfo (UPDATE command) to create a SS-wide coverage which was split according to pool category, providing one polygon coverage of category 1 pools for each focal day. These were then converted to a 1m × 1m grid for use as input in creation of a CPOOL grid using the ArcInfo function PATHDISTANCE in the same manner as the CACC grid.

Table 2.2: Summary of dates on which aerial photographs of the SS were taken. Survey dates have been classified according to the "stage" of the breeding season in which they were performed, as defined in Table 2.1.

Year	Dates collected and analysed (DD/MM)	Stage of Breeding Season
1998	10/10	Early
	17/10	Mid
	25/10	Late
2004	03/10	Early
	16/10	Mid
	26/10	Late
2008	05/10	Early
	17/10	Mid
	29/10	Late
2009	24/10	Late
	03/11	End
2010	30/09	Beginning
	12/10	Mid
	24/10	Late
	03/11	End

2.4.3.3 Pool salinity

Seals have previously been observed drinking from pools of water at North Rona; therefore, salinity was quantified in an attempt to assess whether a preference for less brackish water influenced seal distribution. This is important as sea spray and rainfall have different contributions to pool composition in different areas of the SS; where sea spray has a large contribution to pool volume (e.g. in the north-west of the SS or around access points) the salinity is much higher than elsewhere, and is more similar to brackish seawater than near-freshwater (e.g. up to 22‰ NaCl compared to approximately 1‰). Pool salinities from multiple days of sampling in 2009 and 2010 (Table 2.3) were recorded on base maps of pools from the 1994 breeding season. Salinity was measured in parts per thousand (ppm; ‰), based on the refractivity index of the water sample, using a Bellingham and Stanley Ltd. Eclipse Handheld 45-65 Salinity Refractometer. The 1994 base map was used as, being from later in the season, it had the largest number of pool locations; although not all pools would necessarily be present during the sampling, this map allowed the researcher (PPP and SDT) to get the closest pool to the actual pool sampled, allowing salinity readings to be recorded at an (x,y) (OS GB) location within the GIS accurate to within ±2m. An *ad hoc* sampling regime was used, but one which aimed to sample pools in a range of areas across the SS; this approach was necessary as the sampling was performed whilst researchers were engaged in other activities in the SS (e.g. seal captures and focal observations). These maps of salinity readings were geo-rectified and digitised in the GIS with a single point value representing each salinity reading. As the salinity of every pool present at each survey date could not be measured, the salinity at unmeasured locations was predicted using spatial interpolation of salinity values at known locations. A salinity grid ('surface') for each

stage of the 2009 and 2010 breeding seasons was created using spatial interpolation following the procedure detailed below. To create putative salinity surfaces for 1998, 2004 and 2008 a surface was created for each stage of these seasons which averaged across the corresponding 2009 and 2010 surfaces.

Table 2.3: Summary of salinity data collection dates (DD/MM). "Breeding Season Stage" indicates a classification of datasets based on which aerial survey dates (Table 2.2) the data were collected closest to.

Year†	Dates collected	Breeding Season Stage
2009	5/10, 8/10, 11/10	Early
	15/10, 17/10, 18/10	Middle
	21/10, 24/10, 28/10	Late/ End
2010	29/09, 05/10	Early/ Beginning
	09/10, 11/10, 12/10	Middle
	19/10, 31/10	Late/ End

†Salinity data was not available for 1998, 2004 or 2008. To provide salinity data in further analyses of these years, an average of the 2009 and 2010 data was used.

Interpolation was carried out so that all SS locations could be assigned a salinity value, including those in unsampled regions. All interpolation procedures were performed using POINTINTERP in ArcInfo, utilising an exponential distance-weighted interpolation, which interpolates a grid (surface) from a set of points. POINTINTERP using this method and the SMOOTH function modification of the interpolation weighting creates an output grid whose cell values are determined by their proximity to the input points from the salinity point coverage. Thus the output grid cell value is dependent on both the salinity value and the proximity of the salinity point to the output grid cell's centre. A salinity point will only affect the value of an output cell if it is within a certain "radius" of the output cell's centre, and the SMOOTH function ensures that the 'weight' of input salinity points declines towards zero as its distance from the output cell centre approaches the value of the radius. This results in a Gaussian curve weight function with a weight of 1 at a distance of 0, declining to 0 at the extent of the radius from the input cell centre. Three salinity surfaces were created for focal day, each with a different radius (5m, 20m, 300m). These were then combined such that each cell of the combined grid was assigned the highest value from each of the three grids. This was carried out because the 5m radius provided good "local" interpolation, near to pools, but left a lot of areas with "NODATA" values between the sampled pools; conversely, the cells of the 300m output grid assigned salinity values to all cells in the combined grid, but did not adequately represent the salinity values at sites near to pools, and produced much lower salinity values in the output than were empirically measured. The 20m grid provided an overall more accurate interpolation at intermediate proximities to salinity measurements. Thus, a combination of all three grids provided an interpolated surface most representative of the salinity values measured in the field. Finally, the combined salinity surface was 'masked' to ensure it had the same extent as all other EGV maps (CACC and CPOOL).

2.4.4 Extraction of seal spatial data from GIS database

Seven variables were extracted as text files from the GIS database for subsequent statistical analysis (Section 2.4.7; Chapter 3). These variables were extracted as they may be useful in describing the response of individuals or the population as a whole to changing EGVs:

(i) Distance between each neonate (or weaner; Chapter 5) and it's nearest female (MPdis)
(ii) Distance between each female and its nearest female neighbour (NNdis)
(iii) Elevation at adult female and pup locations and in every 1m × 1m cell of the SS
(iv) CACC at adult female and pup locations and in every 1m × 1m cell of the SS
(v) CPOOL at adult female and pup locations and in every 1m × 1m cell of the SS
(vi) Salinity at adult female and pup locations and in every 1m × 1m cell across the SS
(vii) CFEM at weaner and neonate locations and in every 1m × 1m cell of the SS (Chapter 5).

To calculate MPdis and NNdis, the ArcInfo command NEAR was used, which calculates the distance between specified points in one coverage (for example, pup locations) and those in another coverage (for example, female locations). The speed required during the daily mapping process meant that mother-pup pairs could not be reliably identified in-field. Therefore, the nearest female to each neonate was assumed to be that pups' mother; MPdis is thus assumed to represent the distance between each pup and its mother. For my purposes this seems a reasonable assumption as microsatellite analyses have previously shown that approximately 88% of pups are the offspring of their nearest adult female (Worthington Wilmer *et al.,* 2000). MPdis therefore represents the most conservative possible estimate of actual mother-pup distances (Twiss *et al.,* 2000a). To calculate variables (iii) – (vii), the 'species' distribution of each EGV, the ArcInfo command SAMPLE was used. SAMPLE creates a table showing the values of EGV map grid cells for locations with seals present. This was performed for adult females and neonates for analysis in Chapters 3 and 4, and for weaners for analysis in Chapter 5. Input grids had been processed such that all had the same geographic extent and scale (see Section 2.4.5 for more information). In order to obtain EGV measurements for every grid cell in the SS for these variables (the "global" distribution of each EGV), the ArcInfo command UNLOAD was used. UNLOAD creates a table of EGV values associated with grid cell coordinates. This allows the comparison of EGV values in each location between years and breeding season stages, and allows for a comparison of 'global' and 'species' EGV distributions. The SAMPLE process was repeated, following niche modelling (Chapter 4), to assess the species distribution on modelled HS values.

2.4.5 Species Distribution Modelling

Seal presence and EGV maps (all as 1m × 1m grids) were converted to ASCII files and imported into IDRISI32 (Version I32.11; Clark Labs, The Idrisi Project, 950 Main Street, Worcester MA, USA). IDRISI32 was used to convert the ArcInfo ASCII format maps into raster maps suitable

for use in BioMapper (Version 4.0.7.373; Hirzel *et al.,* 2007), which can only utilise raster format maps. BioMapper implements a suite of GIS and statistical tools using these presence and EGV data for the creation of HS models and maps. All presence and EGV maps were imported to BioMapper and masked to uniformly set the background value to -9999. Maps were 'verified' to remove discrepancies, ensuring that all covered the same extent and that all land and background cells were equivalent across maps. Typically approximately 1200 cells were removed from maps with discrepancies, so all maps subsequently used with BioMapper and other statistical analyses were composed of 82223 1m × 1m cells. The discrepancies that were eliminated (Figure 2.6) were areas unused by, and unavailable to, the seals (in the far north east of the SS or small outcrops a short distance off of the coast); discrepancies therefore represented areas that were not of interest to further analyses and were eliminated. For focal days one species map was used in niche models alongside one of each EGV map for the corresponding date. The use of BioMapper and ecological niche factor analysis (ENFA), the method on which BioMapper is centred, will be fully described and explained in Chapter 4.

Figure 2.6: Outline map of North Rona (land surface in black), showing in red the 'discrepancies' removed from all maps in the verification process prior to analyses. These areas are predominantly rocky outcrops offshore and larger areas in the north-east which are often wave-swept and remain unused by the seals.

2.4.6 Weather data

The weather data used in this thesis included air temperature (°C), rainfall (mm) and mean sea level pressure (MSLP; hPa). Hourly and daily air temperature and MSLP data were obtained from the Met Office's British Atmospheric Data Centre (BADC) for North Rona for all dates in the 1998, 2004 and 2008 breeding seasons. However, corresponding data were not available for North Rona for 2009 and 2010 as the weather station on the island was decommissioned prior to the start of the 2009 breeding season. Therefore, temperature and MSLP data for all five years were obtained for Sule Skerry (59° 05' N, 04° 24' W), a remote skerry 75km east of North Rona and situated on a similar latitude. Figure 2.7 shows the correlations in the daily air temperature and MSLP between North Rona and Sule Skerry for 1998, 2004 and 2008. A significant correlation was found in both weather parameters in all three years (Table

2.4). Therefore, in order to maintain consistency in data sources, the air temperature and MSLP data for Sule Skerry will be used in place of that for North Rona for all years.

Table 2.4: Correlation between weather variables at North Rona and Sule Skerry for 1998, 2004 and 2008 (n=60). Assessed using Pearson's Product Moment Correlation.

Variable	Year	r	*p*
Mean Sea Level Pressure (MSLP)	1998	0.994	<0.001
	2004	0.996	<0.001
	2008	0.994	<0.001
Air Temperature	1998	0.995	<0.001
	2004	0.980	<0.001
	2008	0.992	<0.001

Rainfall data were collected by R.M. Culloch (RMC) using a conical rain gauge located in Fianuis Central in 2008 and 2009; in addition, qualitative observations of the daily rainfall were made for all other seasons by SDT. No rainfall data were available for North Rona from the BADC and the BADC records from surrounding weather stations are incomplete, often comprising only one or two days of data per month. This necessitates a more qualitative approach to the assessment of the influence of rainfall on grey seal distribution in some years. MSLP was analysed as a proxy for rainfall, as in Twiss *et al.* (2002), with higher MSLP indicating drier weather. Wind could also influence seal thermoregulation, by assisting evaporative heat loss. Wind speed and direction data was available for North Rona and Sule Skerry throughout each breeding season, however these were not analysed with respect to seal distribution because it is unknown how much of an effect the wind has on thermoregulation, particularly because seals remain close to the ground, and some may be sheltered from the wind in small hollows (McCafferty *et al.,*2005).

2.4.7 Statistical analyses

All statistical analyses were performed using the freely available 'R' (Version 2.15; R Development Core Team, 2012). R is a language and programme designed to perform statistical analyses and graphical plotting functions. Statistical methods will be described and explained in the relevant sections and where R packages have been used that are not supplied with the base package they will be identified.

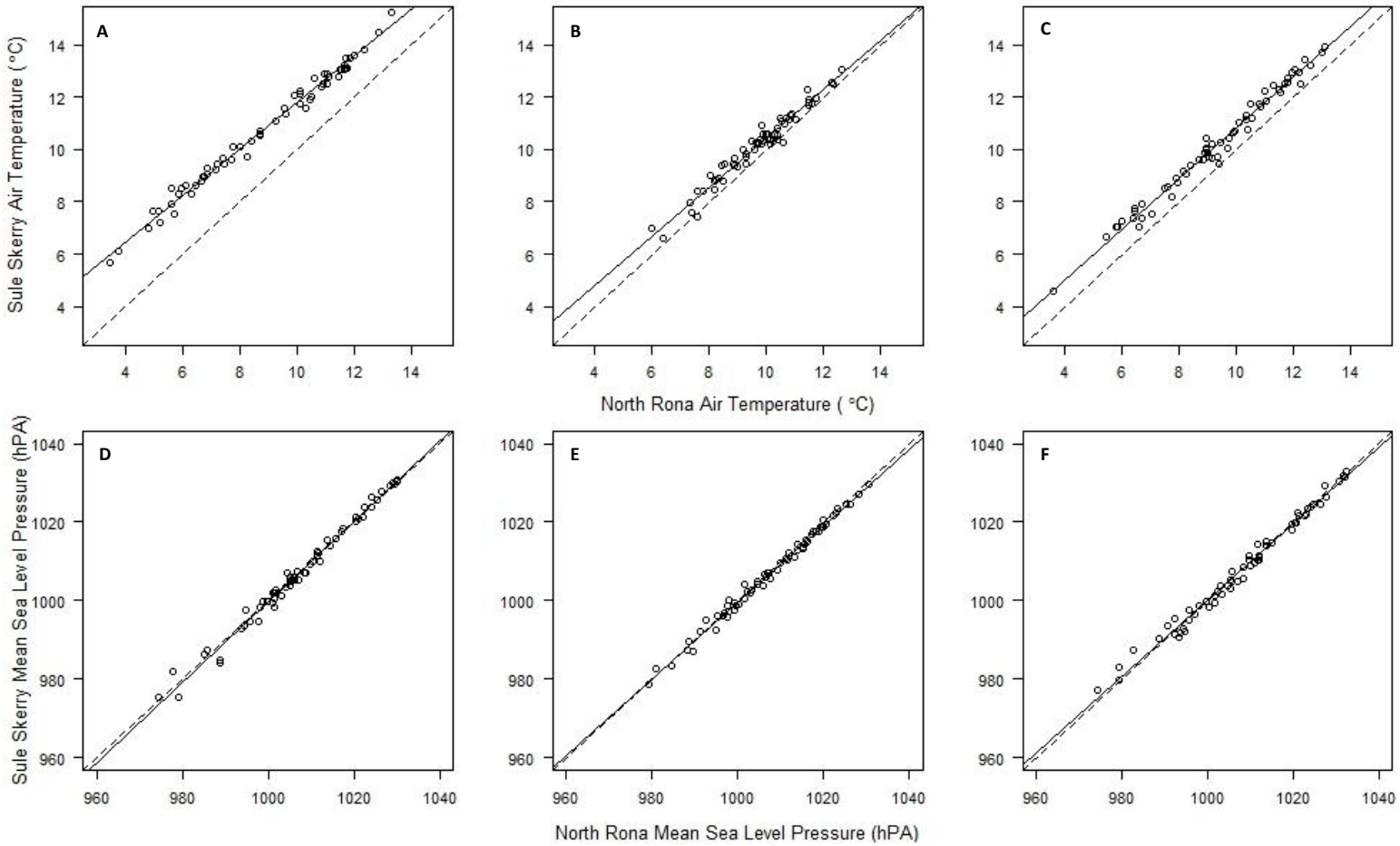


Figure 2.7: Correlation in daily mean air temperature (^{o}C; A-C) and daily mean sea level pressure (hPa; D-F) between North Rona and Sule Skerry for 1998 (A & D), 2004 (B & E) and 2008 (C & F). The dashed line in each figure represents the 1:1 line whilst the solid line represents the regression line of best fit to the data. In all cases the correlation was very strong and positive (Pearson's Product Moment Correlation; r>0.98, N=60, p<0.001); for more details, see Section 2.4.6.

2.5 Summary of terms

Table 2.5: A summary of key technical terms used throughout this thesis, with brief definitions for reference purposes.

Term/ Abbreviation	Definition
EGV	Ecogeographical variable (= environmental descriptor).
CACC	'Cost-distance' to nearest access point.
CFEM	'Cost-distance' to nearest female.
CPOOL	'Cost-distance' to nearest pool.
ELEV	Elevation (metres above sea level).
SAL	Salinity (per mille; ‰).
HS	Habitat suitability
Global distribution/ dataset	Refers to the availability of particular habitat features (EGVs) or habitat suitability (HS) values over the entire study site.
Species distribution/ dataset	Refers to the EGV or HS values recorded at species locations, i.e. is a subset of the global distribution defined by species presence.
NNdis	Distance of an adult female to her nearest adult female neighbour.
MPdis	Distance of an adult female to her nearest pup.
ENFA	Ecological Niche Factor Analysis; compares the global distributions of the EGVs with the species distribution of the EGVs. Summarises the EGVs into uncorrelated (marginality and specialisation) factors. The species distribution on these factors allows the computation of a habitat suitability map.
Marginality	Describes how far the species optimum is from the mean habitat in the study site, calculated by comparing the species distribution with the global distribution for all EGVs.
Specialisation	Describes how specialised the species is by reference to the available range of habitat (EGVs) in the study site, i.e. how narrow, or restricted, the species niche is.
Tolerance	The inverse of specialisation; describes how wide the niche is.
DA	Discriminant analysis; compares the niche of two species, finding the axis along which the niches are most separated.
SDM	Species distribution model
Study Area (SA)	An area in the south of the Fianuis peninsula of North Rona which has been the focus of much ecological research (see Sections 2.3.1-2.3.3); defined by previous researchers based on differences in topography and seal distribution compared to other areas of the Fianuis peninsula.
Study Site (SS)	The site for the research presented in this thesis; incorporates the majority of the SA in addition to the south of 'Fianuis South', the region of Fianuis peninsula north of, and adjacent to, SA.
Females	In relation to grey seals, refers specifically to *adult* females; pup sexes analysed together.
Neonates	In relation to grey seals, refers specifically to the grouping of stage I and stage II pups. These stages were used as they are the least mobile, and so their locations are likely to represent female pupping site locations, and this provides a larger sample size than stage I pups alone.
Weaners	In relation to grey seals, refers specifically to weaned (stage V) pups.

3. Exploratory Data Analysis: Habitat availability, the weather and seal distributions at North Rona

3.1 Introduction

Throughout its range, the grey seal breeds on a wide variety of substrates (Anderson *et al.,* 1975; Stirling, 1975; Boness and James, 1979; Anderson and Harwood, 1985; Haller *et al.,* 1996) and the topography at haul-out sites has been found to strongly influence female distribution. Twiss *et al.* (2000a) concluded that topographical differences between sites are likely to influence pupping site selection in addition to individual behaviour, with consequences for quality and quantity of pup provisioning. North Rona is cliff bound and lacks the beaches seen at many breeding colonies such as the Monach Isles (Anderson and Harwood, 1985); the main breeding area of Fianuis peninsula lies between 2-50m above sea level and consists mainly of undulating grassy terrain punctuated by irregularly spaced fresh to brackish water pools of variable size, boulders and the remains of stone walls (Twiss *et al.,* 2002). The change in elevation over the breeding area is due to a gradual slope increasing from 0^{o} at the top of the access points from the sea to 40^{o} further inland, towards the south of the SS (Twiss *et al.,* 2002). Such qualitative site descriptions have been used in a number of studies, on grey seals at North Rona (Anderson *et al.,* 1975; Anderson and Harwood, 1985) and elsewhere on a range of other taxa, to describe the effects of topography on the distribution of individuals (e.g. southern sea lions, *Otaria flavescens,* and Ipswich sparrows, *Passerculus sandwichensis princeps*; Campagna and Le Boeuf, 1988, Reid and Weatherhead, 1988). These have been useful in determining that female grey seals at North Rona typically aggregate around pools of water and gather in high concentrations around the access gullies (Pomeroy *et al.,* 1994; Twiss *et al.,* 2000a; 2001). However, few studies have quantified the topography at an appropriately fine scale, i.e. that at which individuals interact with their environment (e.g. Twiss *et al.,* 2000a; 2001). Such an approach is important at North Rona given the fine-scale heterogeneity in topography over the SS (PPP and SDT, *pers. comm.*). This heterogeneity interacts with local weather to generate the variable distribution of pools that are thought to influence female distribution.

This chapter aims to quantitatively describe the range and variability of available conditions on North Rona at a sub-seal size spatial grain (Section 3.3.1) in addition to exploring the weather data available for North Rona (Section 3.3.2). General trends and the variability in the geographic distribution of individuals within the colony will then be described (Section 3.3.3) before linking this explicitly to the quantitative description of available habitat (Section 3.3.4). These seal-habitat links will be further explored in Chapter 4 to delineate adult female pupping site and subsequent habitat preferences. Though the general trends in population distribution at North Rona have been previously described (for example, Pomeroy *et al.,* 1994), it is useful to re-

examine this both in light of detailed multi-annual data on the distribution of EGVs over the SS and to see if this has changed over the years as the breeding colony has declined. The long-term GIS database of individual seal locations and access to aerial photos of the SS permits the examination of long-term links between fine-scale habitat and seal distribution that has not previously been possible.

3.2 Methods

EGV data shown in sections 3.3.1 and 3.3.4 and species location data shown in sections 3.3.3 and 3.3.4 were collected and entered to the GIS as described in Section 2.4. The methods for extraction of the data presented below are outlined in Section 2.4.4. Rather than reiterate these methods, the aim of this section is to describe and explain the transformations and statistical analyses performed on the species location and EGV data for exploratory analysis.

3.2.1 Data manipulation and transformations

All summary statistics (averages and standard deviations) and plots (unless stated otherwise) presented in Section 3.3 have been calculated and created using raw, untransformed data. However, for the statistical analyses, much of the data were transformed in order to make them more closely approximate a normal, homoscedastic distribution. Prior to transformation all EGV data (derived from the maps imported into BioMapper) had a constant (a 'shift') of 1 added in order to remove zeros; this was important as the transformations used generally deal poorly with values between zero and one (Osborne, 2002). No shift was applied to daily means of the mother-pup or nearest-neighbour distances as these datasets contained no values less than one; however, transformations towards normality were still applied. Transformations were applied where data was deemed to be severely non-normal and/or heteroscedastic based on visual evaluation of boxplots and Q-Q plots in addition to Fligner-Killeen tests for homogeneity of variances and Shapiro-Wilk tests for normality. Fligner-Killeen tests were used as these are the most powerful tests in the presence of non-normality (Conover *et al.,* 1981), which was common in many of the datasets presented. Shapiro-Wilk tests for normality were chosen as this method has been shown to be the most powerful in comparison to other common normality tests (Kolmogorov-Smirnov , Lilliefors and Anderson-Darling tests; Razali and Wah, 2011).

Table 3.1 indicates the transformations applied to the 'global' and 'species' datasets prior to statistical analyses. The transformation was used which would best produce normality and heteroscedasticity in the transformed data, and was determined by investigation of the skewness and kurtosis exhibited by each dataset. It was important to apply the same transformation to all data within a dataset (i.e. apply the same transformation to all salinity values regardless of breeding season or stage of breeding season) so that each part of the dataset could be compared

following transformation. Following transformation the data were again visually assessed using boxplots and Q-Q plots, and were further assessed for normality and heteroscedasticity using the Shapiro-Wilk and Fligner-Killeen tests.

The whiskers on all boxplots show the value farthest from the median that is within 1.5 times the inter-quartile range (IQR) of the upper and lower quartiles. A number of 'outliers' are present in the EGV data, where outliers are defined as those data points further from the median than 1.5IQR (R Development Core Team, 2012). However, here I take the definition of 'outlier' from Dixon (1950:488) as being a data point that is "'dubious' in the eyes of the analyst" and conclude that the apparent outliers in the EGV data represent real (i.e. not 'dubious') data at locations accessible to seals; therefore, it was not deemed appropriate to remove extreme values from either the global or species datasets as the full dataset is likely to be more representative of reality (Orr *et al.,* 1991). It is important to correctly asses and quantify the entire accessible area in studies such as this (Barve *et al.,* 2011), and in the global dataset the extreme EGV values represent geographic areas that females could reasonably gain access to (PPP and SDT, *pers. comm.*) and which they may therefore reasonably encounter during their haul-out. Furthermore, due to the nature of the recording regime (Section 2.4.2), it is unlikely that species locations were incorrectly recorded and it seems appropriate to take account of the full range of conditions encountered by individuals. The transformations outlined above were used to reduce the skew and error variance in the data caused in part by these more extreme values.

Table 3.1: Summary of transformations applied to each quantitative variable.

Variable	Abbreviation	Shift	Transformation
Cost-distance to access	CACC	+1	Square root
Cost-distance to nearest pool	CPOOL	+1	Natural logarithm
Elevation	ELEV	+1	Square root
Salinity	SAL	+1	Inverse
Mother-pup distance	MPdis	+1	Inverse
Distance to nearest adult female neighbour	NNdis	+1	Inverse

The above shifts and transformations were applied to the global and species (both females and pups) datasets prior to any statistical analysis.

3.2.2 Statistical analyses

In general, the R package 'MULTCOMP' (Hothorn *et al.,* 2008; Herberich *et al.,* 2010) was used for multiple comparisons of means. MULTCOMP uses a new multiple comparison procedure which makes no assumptions on the distribution, sample size or homoscedasticity of the input data (Hothorn *et al.,* 2008). MULTCOMP performs multiple comparisons similar to post-hoc (e.g. Tukey's) tests based on an ANOVA model and returns the *p*-value associated with each contrast. Pairwise comparisons of means can therefore be simultaneously carried out whilst controlling the

probability of making a Type I error (falsely rejecting one or more hypotheses). Prior simulations to assess the performance of this procedure have shown that the Type I error rate is well controlled even under conditions of unbalanced designs, non-normality and heteroscedasticity (Herberich *et al.,* 2010) and therefore does not suffer from the increased false positive results produced by standard comparisons of means in unbalanced designs (Herberich *et al.,* 2010). Despite this, data were transformed towards normality prior to analysis, since the performance of even non-parametric tests can benefit from transformations to improve normality (Osborne, 2010). For the comparison of two datasets, Mann-Whitney U tests were used. The choice of statistical test in each instance is indicated in the appropriate section. Statistical tests were performed on transformed data and the reported results of all statistical tests are from tests on transformed data (even where plots are presenting raw, untransformed data). However, where inverse transformations were applied, results of statistical tests are stated in terms of the untransformed, rather than transformed, data for ease of comprehension (i.e. the direction of correlations reflects the real data).

3.2.3 Female and pup proximity analyses

The NNdis and MPdis for all females were calculated for all dates in each breeding season. When NNdis and MPdis were used as a dependent variable in relation to the 'stage' of breeding season, only the NNdis and MPdis for the appropriate focal dates were considered. However, to describe changes in NNdis or MPdis in relation to the day of the breeding season or prevailing weather conditions, the full dataset was used. To describe the pattern of dispersion in adult female seal locations, the observed mean NNdis ($\bar{d}_{obs;}$ untransformed) obtained for every day of all five breeding seasons was compared with the expected mean NNdis for a random arrangement ($\bar{d}_{ran}$; Equation 3.1) and maximally dispersed arrangement ($\bar{d}_{dis}$; Equation 3.2) for the same number of points over the same area.

$$\bar{d}_{ran} = \frac{1}{2\sqrt{p}} \qquad \text{(Equation 3.1)}$$

See Clark and Evans (1954) for the derivation of this equation.

$$\bar{d}_{dis} = \frac{2^{\frac{1}{2}}}{3^{\frac{1}{4}}\sqrt{p}} = \frac{1.07453}{\sqrt{p}} \qquad \text{(Equation 3.2)}$$

In addition, to provide a more concise measure of pattern, the nearest neighbour index '*R*' was calculated for each day (Equation 3.3).

$$R = \frac{\bar{d}_{obs}}{\bar{d}_{ran}} \qquad \text{(Equation 3.3)}$$

Values of *R* can range between 0.00 (complete clustering, NNdis = 0.00) and 2.15 (complete dispersion; maximum possible distance between each point, dependent on number of points within the SS), with a random pattern indicated by *R* = 1.00. The value for *R* is tested for significance by comparison with critical values for *R* (Table A1.1, Appendix 1) (Ebdon, 1976; Ebdon, 1985) and the test statistic '*c*' (Equation 3.4), the calculation of which is similar in form to Student's *t*.

$$c = \frac{\bar{d}_{obs} - \bar{d}_{ran}}{SE_{\bar{d}}} \qquad \text{(Equation 3.4)}$$

The test statistic *c* is a standard normal deviate, the significance of which can be tested by comparison with the table of critical values given in Table A1.2 (Appendix 1). In equations 3.1 – 3.5, *p* is the density of points (seals), per unit area (the number of observed points divided by the area of the SS); $SE_{\bar{d}}$, derived as per Equation 3.5, is the standard error of the daily mean NNdis ($\bar{d}_{obs}$) and is analogous to the ordinary standard error of the mean (Ebdon, 1985).

$$SE_{\bar{d}} = \frac{0.26136}{\sqrt{np}} \qquad \text{(Equation 3.5)}$$

The factors influencing the change in *R* were investigated for each season using correlations and a GLM (Gaussian family, link identity) with *R* as the dependent variable and MSLP, air temperature, number of females ashore and day of breeding season as additive predictors. Model selection was performed from amongst all possible combinations of variables based on the Δ-AIC values, where each Δ-AIC value is equal to the corresponding AIC value minus the smallest AIC value (the smallest AIC therefore equates to a Δ-AIC of zero). Following the criteria of Richards (2008), the most parsimonious of the models with Δ-AIC values of less than or equal to six was selected as the 'best' model. In other words, models within six Δ-AIC points of the 'best' model were retained within a preliminary confidence set and the best model was chosen from amongst these based on the model structure, rejecting 'nested' models (where a model is considered 'nested' if it contains the same terms as a simpler model and one additional term).

3.3 Results

The majority of boxplots presented in this section have had 'outliers' removed for clarity. Corresponding figures including outliers may be found in Appendix 2 where indicated; these are important as they show the full range of EGV values available to the seals. Tables and figures are presented at the end of the appropriate sections to avoid breaking up the text.

3.3.1 Description of available habitat

Following all necessary clipping and validating of the EGV maps (Section 2.4.5), the SS was composed of a total of 82223 × $1m^2$ cells, each of which was assigned values relating to the four EGVs being considered in these analyses; elevation, CACC, CPOOL and salinity. As CACC and elevation relate directly to the permanent topography of the SS, the global distribution of these variables are constant throughout and between each breeding season; conversely, CPOOL and salinity are variable throughout and between breeding seasons. Tables 3.2 – 3.3 present the means and standard deviations of CPOOL and salinity over the SS for each stage of every breeding season; to prevent repetition in Section 3.3.3, Tables 3.2 – 3.3 also present these summary statistics for females and neonates for the corresponding dates; these are presented separately for elevation and CACC in Section 3.4. Each EGV will be examined in turn in Sections 3.3.1.1-4.

3.3.1.1 Elevation

The SS is generally low-lying (mean = 17.39m; Figure 3.1a), though there is considerable variation about this mean (standard deviation = 12.09) with a range of elevation from 0 at the access points to 66.2m in the southwest of the SS (Figure 3.1b; Figure A2.1, Appendix 2.1.1, shows the full range of elevation over the SS). Only 10.3% of the SS has very low elevation (0-5m above sea level), which is mostly found around the access points in the east of the SS (Figure 3.1b).

3.3.1.2 'Cost-distance' to nearest access

On average, locations within the SS are relatively low 'cost' in terms of travel towards the access points (mean CACC = 31.64; Figure 3.2a), though there is considerable variation about this mean (standard deviation = 22.36) with a range of CACC from 0 at the access points to 100 in the southwest of the SS (the CACC values were scaled from 0-100; Figure 3.2b). This is reflected in Figure 3.2a, which indicates that high CACC values are uncommon relative to lower values across the SS (Figure A2.2, Appendix 2.1, shows the full range of CACC over the SS).

3.3.1.3 'Cost-distance' to nearest pool

The 'average' location in the SS is relatively low 'cost' in terms of travel towards the nearest pool (CPOOL = 14.79 on average (mean of the means from each focal day); Table 3.2), and

high CPOOL values are uncommon relative to lower values (Figure 3.3). There is considerable variation about this mean, both between breeding season stages (means range from 11.90 – 17.99; Table 3.2) and within stages (standard deviations range from 10.02 – 19.42; Table 3.2), with a range of CPOOL values from 0 (within pools) – 95.32 in 1998, 0 – 74.86 in 2004, 0 – 104.90 in 2008, 0 – 134.66 in 2009 and 0 – 100.26 in 2010. These values represent the absolute maximum CPOOL observed within each breeding season. The maximum CPOOL is variable between stages of each breeding season (Table 3.2). There does not appear to be a consistent trend in CPOOL change within seasons though in general the study site gets wetter over the season; in 1998 and 2008-2010 there is a decrease in CPOOL towards the end of the season (i.e. pools are more readily available, covering more of the SS), whilst CPOOL values in 2004 show an interesting trend in that they increase consistently over the season, indicating a greater abundance of pools at the start of the season. As detailed in Appendix 2 (Section A2.1.3), the majority of these changes in CPOOL between stages within breeding seasons were significant at least at the $\alpha = 0.05$ level. In general, it appears that pools become more abundant over the season as the SS becomes wetter; this is likely to be related to the weather conditions on North Rona (Section 3.3.2).

3.3.1.4 Salinity

Overall, the SS has relatively low salinity (0.95‰ on average (an average of the mean of interpolated surfaces from each focal day); Table 3.3), though there is considerable variation about this mean, both between breeding season stages (means range from 0.83 – 1.24‰) and within stages (standard deviations range from 0.76 – 1.90). This is reflected in Figure 3.4, which indicates that high salinity values are uncommon relative to lower values. However, not reflected in Table 3.3 or Figure 3.4 is the true extent of the variation in salinity, which ranges from near fresh to brackish: 0 – 16‰ in 1998, 2004 and 2008, 0 - 22‰ in 2009 and 0 - 10‰ in 2010 (these values represent the absolute maximum salinity observed within each breeding season, which is variable between stages of each breeding season). Clearly this is considerable variation, which will likely become important in statistical analyses including niche models (Chapter 4). The higher values in this range of salinity typically occur in the north-west of the SS, and in the east near to access points (Figure 3.4b). Within each breeding season, there is a trend for increasing salinity as the season progresses; as detailed in Appendix 2 (Section A2.1.4) these increases in salinity between stages within breeding seasons were significant at the $\alpha = 0.01$ level. However, the late and end stages of 2009 and the late and end stages of 2010 did not differ as the salinity surfaces used for these stages were identical due to limited data availability (Section 2.4.3); in addition, the same trend is seen throughout 1998, 2004 and 2008 as they use the same set of salinity surfaces.

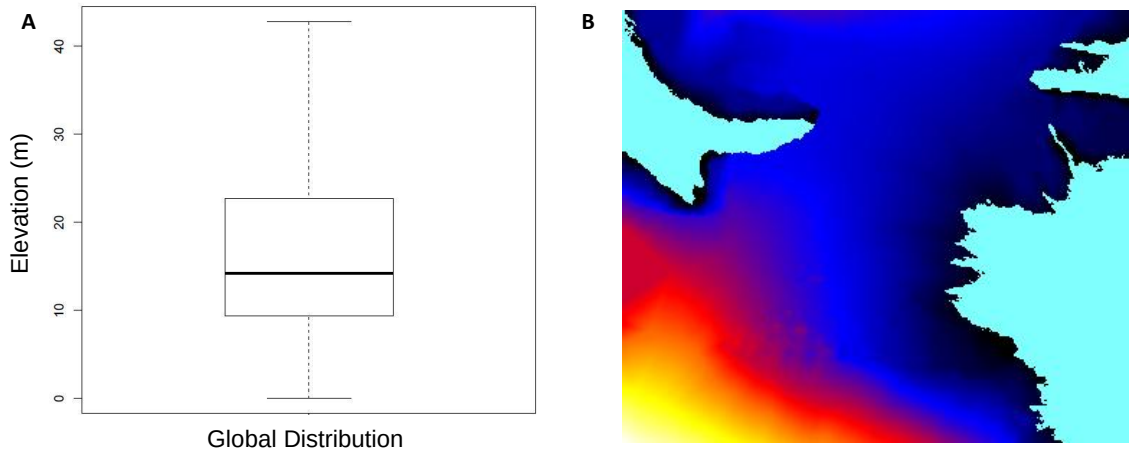


Figure 3.1: Global distribution of elevation (m) across the SS. **A:** See Appendix 2, Figure A2.1 for a corresponding boxplot containing the outliers. **B:** Elevation profile of the SS in geographic space. Dark colours represent low ELEV, whilst the higher values are represented by intense yellows and reds.

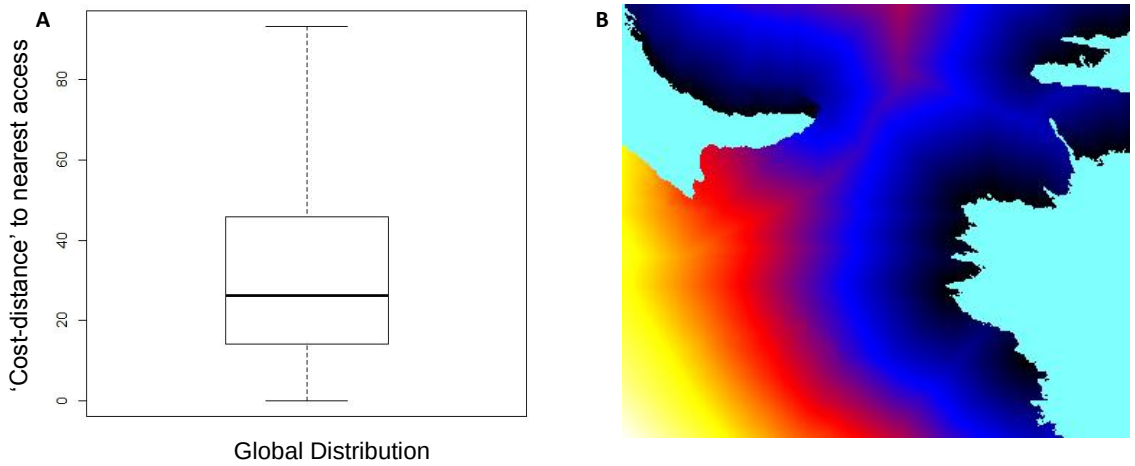


Figure 3.2: Global distribution of 'cost-distance' to access (CACC) values across the SS. **A:** See Appendix 2, Figure A2.2 for a corresponding boxplot containing the outliers. **B:** CACC profile of the SS in geographic space. Dark colours represent low CACC, whilst the higher values are represented by intense yellows and reds.

Table 3.2: Means and standard deviations (SD) of the 'global', female and neonate 'cost-distance' to pool (CPOOL) distributions. Female and neonate distributions show the CPOOL at specific sites where these individuals are present.

Year	Period	Females†		Neonates†		Global	
		Mean	SD	Mean	SD	Mean	SD
1998	Early	10.24	10.40	9.73	8.43	15.89	13.02
	Middle	6.68	5.87	6.79	5.80	11.90	10.02
	Late	9.45	8.50	9.66	8.28	12.48	10.84
2004	Early	3.79	3.70	4.92	4.21	12.28	10.33
	Middle	4.83	5.06	6.20	5.98	14.70	13.11
	Late	7.48	7.40	8.58	8.06	16.55	15.59
2008	Early	9.20	7.54	6.90	6.35	16.11	13.14
	Middle	7.16	8.03	7.75	8.96	16.75	14.44
	Late	6.75	5.38	5.89	5.25	13.41	12.59
2009	Late	10.70	10.06	11.89	10.88	17.99	13.07
	End	5.62	5.42	7.15	6.50	15.95	19.42
2010	Beginning	3.34	1.86	3.53	2.59	14.13	13.63
	Middle	5.13	5.63	6.80	7.61	16.67	12.95
	Late	7.73	7.65	7.78	7.64	16.27	13.32
	End	6.49	6.58	8.88	7.22	10.71	10.03
Mean		6.97	-	7.50	-	14.79	-

†See Section 3.3.4 for an exploration of the species distribution on each EGV.

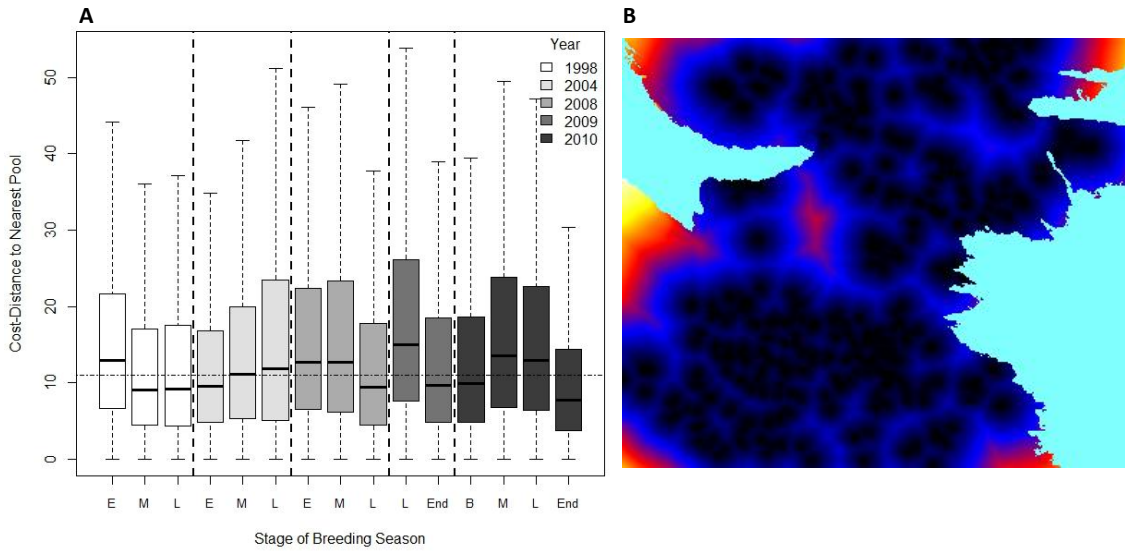


Figure 3.3: A: Global distribution of 'cost-distance to pool' (CPOOL) values across the SS for all seasons. 'B': Beginning; 'E': Early; 'M': Mid; 'L': Late. Horizontal dashed line represents the median CPOOL value over all stages analysed. The whiskers show the value farthest from the median that is within 1.5IQR (inter-quartile range) of the upper and lower quartiles respectively. See Appendix 2, Figure A2.3 for a corresponding boxplot containing the outliers. **B:** Global distribution of CPOOL across the SS in geographic space on 03/11/2010 ("End" 2010). Dark colours represent low CPOOL whilst the higher values are represented by intense yellows and reds.

Table 3.3: Means and standard deviations (SD) of the global and seal (females and neonates) distributions of salinity (‰) across the SS. The female and neonate distributions refer to the salinity at specific location where females and neonates are present.

Year	Period	Females†		Neonates†		Global	
		Mean	SD	Mean	SD	Mean	SD
1998	Early	0.65	0.86	0.63	0.72	1.20	1.87
	Middle	0.68	0.81	0.65	0.75	0.85	1.13
	Late	1.00	1.44	1.03	1.26	1.04	1.53
2004	Early	0.73	1.46	0.85	1.31	1.20	1.87
	Middle	0.86	1.08	0.63	0.88	0.85	1.13
	Late	0.90	0.99	0.63	0.74	1.04	1.53
2008	Early	0.51	0.85	0.51	0.64	1.20	1.87
	Middle	0.75	0.66	0.73	1.22	0.85	1.13
	Late	0.77	0.78	0.70	0.88	1.04	1.53
2009	Late	1.36	1.92	1.48	2.15	1.24	1.90
	End	1.34	1.57	1.33	1.42	1.24	1.90
2010	Beginning	0.06	0.20	0.02	0.04	0.38	0.96
	Middle	0.55	0.68	0.49	0.62	0.53	0.76
	Late	0.70	1.15	0.80	1.22	0.83	1.37
	End	0.72	1.36	0.51	0.66	0.83	1.37
Mean		0.77	-	0.73	-	0.95	-

†See Section 3.3.4 for an exploration of the species distribution on each EGV.

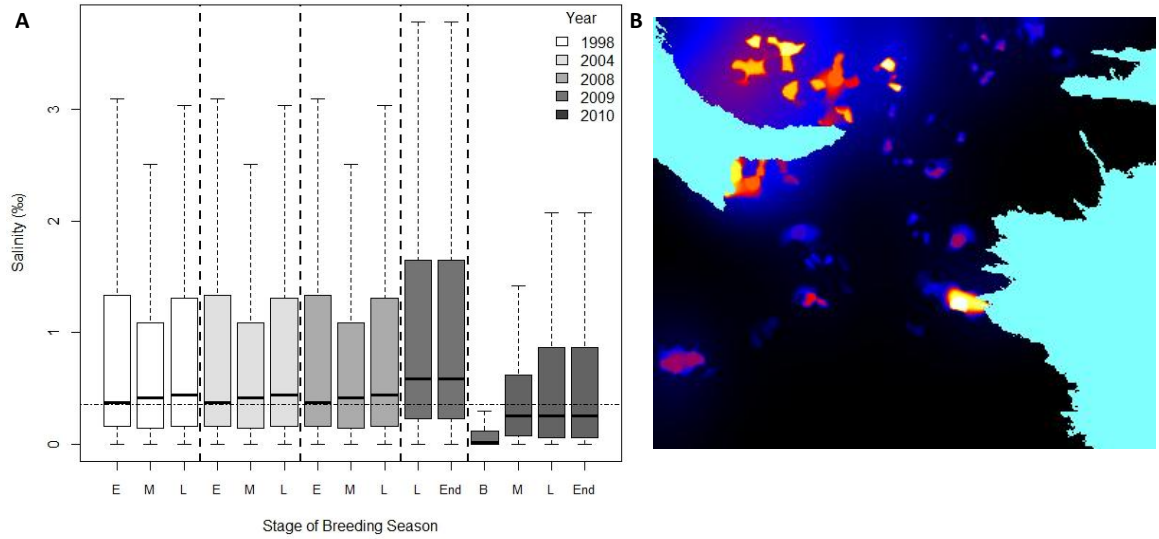


Figure 3.4: Global distribution of salinity (‰) across the SS for all seasons. **A:** 'B': Beginning; 'E': Early; 'M': Mid; 'L': Late. The horizontal dashed line indicates the SAL median for all stages analysed. Outliers removed for clarity; see Appendix 2, Figure A2.4 for a corresponding boxplot containing the outliers. **B:** Global distribution of SAL across the SS in geographic space on 03/11/2010 ("End" 2010). Dark colours represent low salinity whilst the higher values are represented by intense yellows and reds.

3.3.2 Weather data

North Rona has an average daily air temperature of approximately 10°C during the autumn breeding season, and an average MSLP of approximately 1006hPa (Table 3.4, Figure 3.5) throughout the five breeding seasons analysed (using Sule Skerry data as a proxy for North Rona weather data). For years in which quantitative rainfall data were available, there was an average reainfall of approximately 5mm day^{-1}, though this is typically very intermittent. Although there appears to be some inter-annual variation in these averages, inter-annual comparisons (using Kruskal-Wallis and Mann-Whitney U tests) indicated no significant differences between the seasons in air temperature, MSLP or rainfall (Figure 3.5). However, analysing the weather data on a seasonal basis in this way and looking only at means masks the high degree of intra-seasonal diurnal variability in each of the weather variables (Figures 3.6 - 3.8).

During the 1998, 2008 and 2010 breeding seasons, air temperature declines significantly over the season (Figure 3.6); in 2004 there appears to be a similar trend, though Spearman's rank correlation indicates that this is non-significant (Figure 3.6). Contrary to this trend, air temperature increases over the 2009 season. This rise in air temperature towards the end of 2009 is concurrent with a general decline in daily rainfall throughout the season (Figures 3.6 and 3.7), leading to warmer, drier conditions on the colony later in the season than earlier in the season. However, it appears that there was heavy rainfall after quantitative rainfall measurements had stopped, as the global CPOOL average in 2009 is much lower at the "end" of the season (Figure 3.3) than "late" in the season, suggesting much wetter conditions on the colony. Qualitative weather assessments in 2009 also stop too early to be informative in this case (Table A2.3;

Appendix 2). Rainfall does not appear to show a consistent trend for increase or decrease over the 2008 season, though Figure 3.7 suggests that it is generally drier earlier in the season; this is supported by a comparison of the global distribution patterns of CPOOL between early and late in the season (Figure 3.3). When all seasons are considered together, a weak negative correlation suggests that MSLP declines over the breeding season (Figure 3.8); however, when each season is analysed individually, there is only a strong and significant correlation in 1998 (Figure 3.8).

Table 3.4: Summary statistics for weather data (28th September to 4th November annually). For full weather data see Table A2.3 and A2.4 (Appendix 2).

Year	Air Temperature (°C)		Mean Sea Level Pressure		Rainfall (mm)	
	Mean	SD	Mean	SD	Mean	SD
1998	10.9	1.9	1007.4	12.4	-	-
2004	10.1	0.9	1004.7	12.2	-	-
2008	9.7	2.0	1002.6	9.4	4.7	5.1
2009	10.6	1.3	1010.4	12.6	5.8	6.5
2010	10.4	1.9	1006.5	14.3	-	-

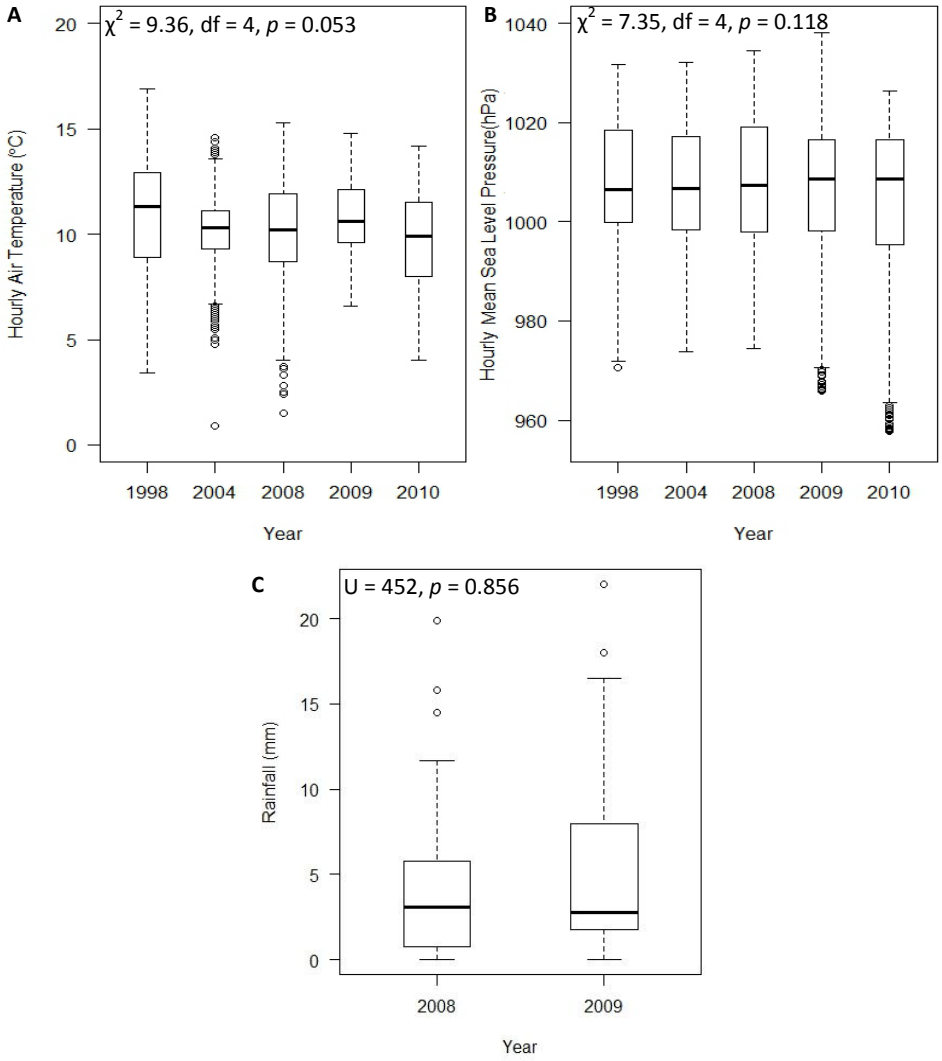


Figure 3.5: Patterns in general weather conditions across all breeding seasons. **A:** Hourly air temperature; **B:** Hourly Mean Sea Level Pressure; **C:** Rainfall (2008 and 2009 only). Kruskal-Wallis tests indicate no change in mean air temperature or MSLP between seasons, whilst Mann-Whitney U tests indicate no difference in mean rainfall between seasons.

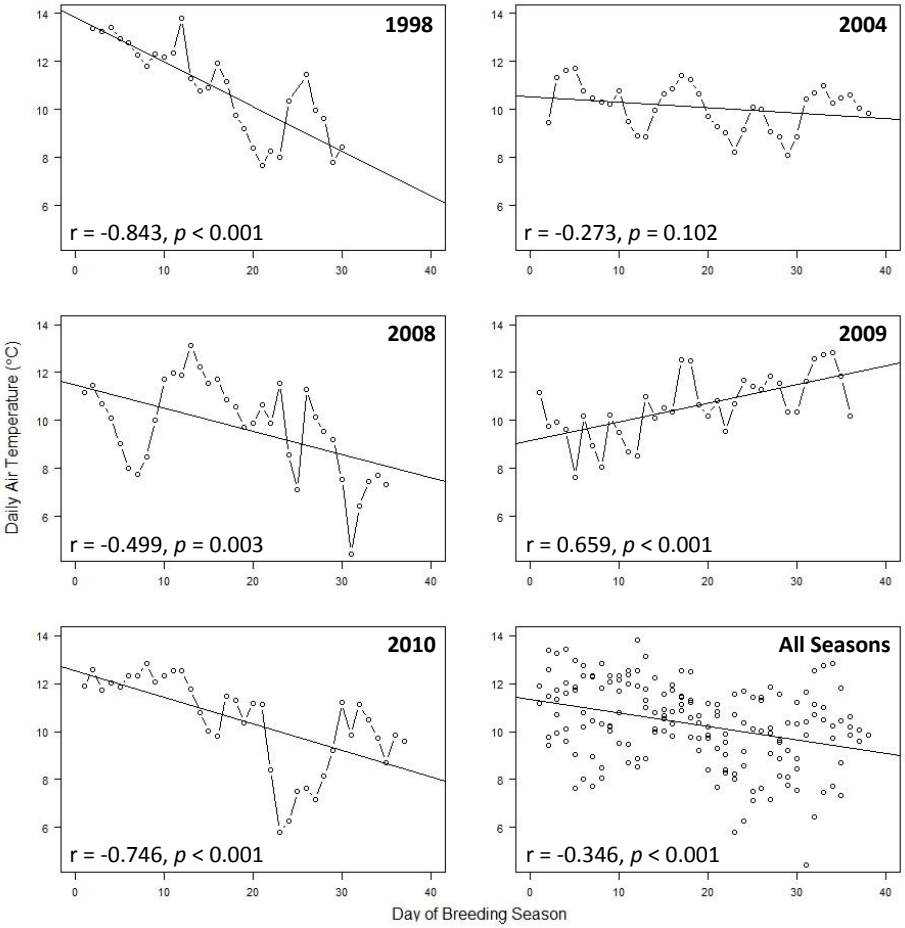


Figure 3.6: Change in air temperature (°C) over each breeding season. Day 1 = 28th September. Spearman's rank correlation indicates that over all seasons there is a negative correlation between air temperature and day of breeding season, a trend shown in 1998, 2008 and 2010; however, there is no correlation in 2004 and a strong positive correlation in 2009, with increasing temperatures towards the end of the season.

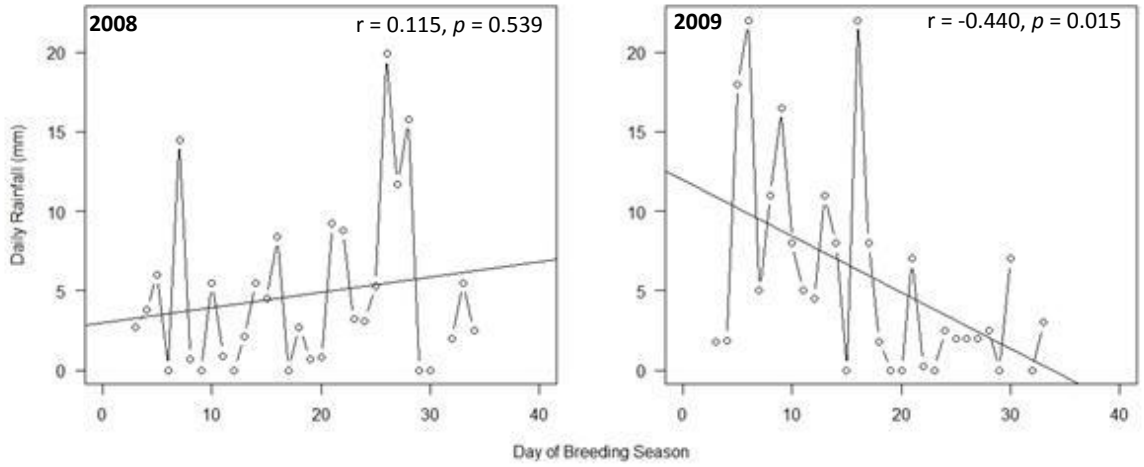


Figure 3.7: Change in daily rainfall (mm) over 2008 and 2009. Day 1 = 28th September. Spearman's rank correlation indicates a negative correlation between daily rainfall and day of breeding season in 2009 only.

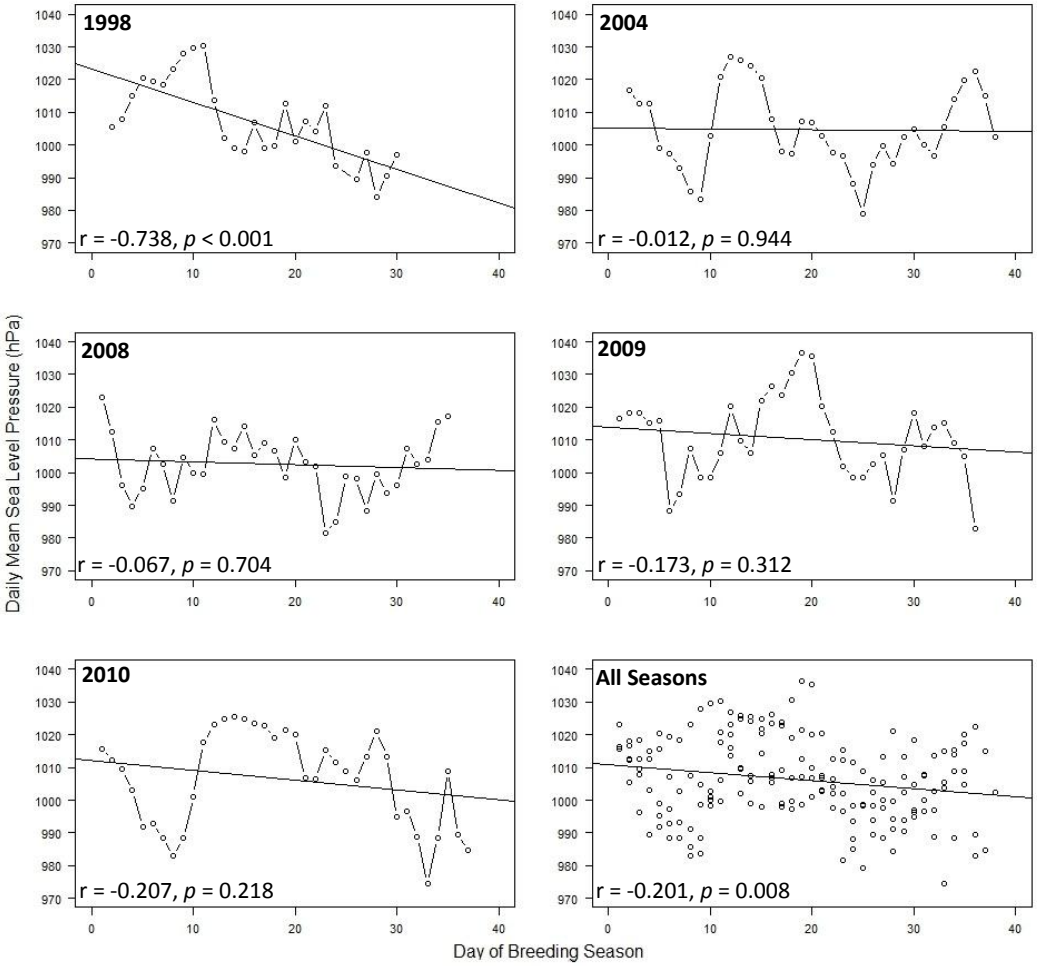


Figure 3.8: Change in MSLP (hPa) over each breeding season. Day 1 = 28th September. There is a weak negative correlation between MSLP and day of breeding season over all seasons (Spearman's rank correlation); however, when analysed individually, there is only a significant correlation in 1998.

3.3.3 Population trends in distribution patterns

Figure 3.9 shows the change in number of individual females ashore throughout the five seasons considered, with a peak in number of females ashore typically occurring around 18th-20thOctober. It is interesting to note from Figure 3.9 and Table 3.5 that there are substantially more individuals ashore in 1998 than in any other year; furthermore, there is a consistent trend for decreasing numbers of individuals ashore in later years, supporting the suggestion that the North Rona breeding colony has been in decline over recent years (Duck and Morris, 2011; CDD and PPP *unpubl. data*). In addition to a decline in the number of individuals ashore, Table 3.6 indicates that less geographical space is being used within the SS in later years, as females maintain similar nearest-neighbour and mother-pup distances in each season.

Over all years and stages of the breeding season, individuals remain in close proximity to their nearest female neighbour (Figure 3.10) and their nearest pup (Figure 3.11), maintaining an average NNdis of 5.52m (± 4.73m; SD) and an average MPdis of 3.40m (± 3.29 m; SD). These figures change little when all dates from each breeding season are considered: females maintain a mean NNdis of 5.99m (±1.26m; SD) and a mean MPdis of 3.48m (±0.77m; SD). There is a negligible

positive correlation (Figure 3.12) between MPdis and NNdis on focal dates (Pearson's product-moment correlation; r = 0.144, df = 1218, $p < 0.001$), when analysed on an individual basis (i.e. in Figure 3.12, each point represents the MPdis and NNdis of an individual female rather than presenting a population average). MULTCOMP analyses, performed on data from focal dates only, also indicated that average NNdis changed significantly between breeding season stages during each season (Figure 3.10) and post-hoc comparisons indicated that average NNdis increased between the breeding season stages within each season (see Appendix 2, Section A2.3.1). Only the increases in NNdis between mid-late 1998, beginning-mid 2010 and mid-late 2010, were not significant. However, in both 1998 and 2010 there is a significant overall increase in NNdis between early and late in the season, consistent with all other seasons. MULTCOMP analysis showed that there were no significant differences in MPdis between breeding season stages within each breeding season (Figure 3.11), with the exception of 2004. Post-hoc multiple comparisons (Appendix 2, Section A2.3.2) revealed a significant decrease in MPdis between early-mid and early-late 2004 (Figure 3.11); this is a trend that can also be seen in the other breeding seasons. This approach to analysing NNdis and MPdis, focusing only on focal dates, is necessary to inform the results of niche models (Chapter 4), which are based on data from focal dates only; the availability of additional data pertaining to the rest of the breeding season also allows a more continuous analysis of change in these variables.

Within each season, when all dates are analysed, there is no consistent correlation between MPdis and day of breeding season (Appendix 2, Section A2.3.3; Figure A2.5), suggesting that, on average, MPdis is constant across the season. In 1998 and 2004, MPdis declines as more females come ashore, though this is trend is not apparent in 2008-2010 (Figure 3.13); this may be a result of the fact that there are fewer females ashore throughout 2008-2010 than in 1998 or 2004 (Table 3.5). It is possible that, due to dry conditions on the colony at the beginning of the 1998 and 2004 seasons (Appendix 2, Table A2.4), females were on average further from their pups during these times due to commuting to scattered pools. No CPOOL data is available for the beginning of 1998 to verify this, though the CPOOL data for early 2004 suggests that females were indeed close to pools during this time (Section 3.3.4; Appendix 2, Section A2.4.3; Figure A2.16).

As each season progresses, there is an increase in mean NNdis (Figure 3.14), with a weak positive correlation between mean NNdis and day of breeding season; the strength of this correlation varies from year to year and is strongest in 2008 (Figure 3.14). There is also no consistent correlation between mean NNdis and mean MPdis, though all significant correlations indicate that females further from their nearest neighbour are also typically further from their pup (Figure 3.15). The increase in NNdis over each breeding season (Figure 3.14) occurs despite the increase in the number of individuals ashore as the season progresses (Figure 3.9), which appears to have no significant relationship with NNdis (Pearson's product-moment correlation; r =

-0.130, df = 1218, $p = 0.651$), and is likely a result of expansion of the colony inland. However, the effect size is clearly very small (Figure 3.14), and this may not be ecologically significant.

Although NNdis only correlates weakly with day of breeding season, there is evidence for a decrease in degree of aggregation as the breeding season progresses: adult female seals are initially highly aggregated but disperse more widely over the SS as the season progresses. Figure 3.16 illustrates this change in distribution of females on North Rona in 2010, which is typical of that seen each year on North Rona. Initial colonisers are relatively clustered at sites near to access points; individuals arriving later in the season tend to move further inland, dispersing away from the main access points in the west. Later in the season the degree of clustering of females decreases as nearest-neighbour distances increase (PPP and SDT, *pers. comm.*). Comparison of observed mean NNdis ($\bar{d}_{obs}$) obtained for every day of all five breeding seasons with the expected mean NNdis for a random arrangement of points ($\bar{d}_{ran}$) and the expected mean NNdis for a maximally dispersed arrangement of points ($\bar{d}_{dis}$) indicated a higher degree of clustering on all dates than would be expected by chance, as the values in the range of $\bar{d}_{obs}$ (3.37 – 9.46m) were substantially smaller than those of $\bar{d}_{ran}$ (6.92-24.96m) or $\bar{d}_{dis}$ (14.88 – 53.64m) on the corresponding dates (Appendix 2, Section A2.3.3; Table A2.6).

To provide a more concise measure of pattern, the nearest neighbour index '*R*' was calculated for each day. Throughout the five breeding seasons, *R* ranged between 0.191 and 0.780 (mean = 0.539 ± 0.121SD), demonstrating a high degree of clustering in seal locations throughout each season. All *R* values (Appendix 2, Section A2.3.3; Table A2.7) were significant at the $\alpha = 0.001$ level whether assessed based on critical values for *R* or the test statistic *c* (see Tables A1.1 and A1.2, Appendix 1, for tables of critical values). Seasonal mean values of *R* did not differ between seasons (ANOVA; $F_{4, 167} = 1.509$, $p = 0.202$), indicating that females maintained a similar degree of aggregation between years despite there being fewer females ashore in later years (Table 3.5). In every year there was a strong positive correlation between *R* and day of breeding season (Figure 3.17), indicating that females were initially highly clustered but became more randomly dispersed throughout each season, a correlation which held when all years were analysed together. *R* also correlated with daily air temperature, mean sea level pressure and the number of females ashore during a number of years (see Appendix 2, Section A2.3.3 and Figures A2.6 – A2.8); however, these correlations were absent where these variables did not also correlate with the day of breeding season, suggesting that the degree of aggregation is linked more directly to day of breeding season than to these variables. Indeed, a GLM performed on these variables demonstrated that in all seasons female grey seals became more randomly dispersed (i.e. *R* increased) as the season progressed (day of breeding season increased), though there was also an effect of the number of females ashore in 2004, 2008 and 2009, whereby an increase in number of females ashore contributes to increasingly random female dispersion (Table 3.7). None of the

best models included MSLP or air temperature as significant predictors of *R* (Table 3.7). Furthermore, *R* did not correlate with daily rainfall in either 2008 or 2009, the only two years with quantitative rainfall data (Appendix 2, Section A2.3.3; Figure A2.9). Finally, in 1998, 2004 and 2010, mother-pup distance declined as the degree of aggregation increased. However, this pattern was reversed in 2008 and 2009 (Figure 3.18).

Table 3.5: Counts of all females and pups within the SS boundaries on focal dates and dates of maximum occupancy, in addition to the maximum number of 10 × 10m grid cells occupied.

Year	Breeding season stage	Count			Maximum number of females ashore	Maximum number of occupied grid cells
		Females	Neonate pups (stages 1 and 2)	Stage I-V pups		
1998	**Early**	296	109	144	430 (on 20/10/98)	245 (on 21/10/98)
	Middle	376	197	298		
	Late	418	133	406		
2004	**Early**	142	60	69	272 (on 18/10/04)	164 (on 23/10/04)
	Middle	258	160	240		
	Late	212	113	286		
2008	**Early**	180	53	62	228 (on 14/10/08)	146 (on 24/10/08)
	Middle	204	121	173		
	Late	175	71	232		
2009	**Late**	175	81	225	216 (on 20/10/09)	137 (on 22/10/09)
	End	112	50	216		
2010	**Beginning**	48	19	24	183 (on 19/10/10)	116 (on 21/10/10)
	Middle	135	86	112		
	Late	176	59	178		
	End	106	41	193		

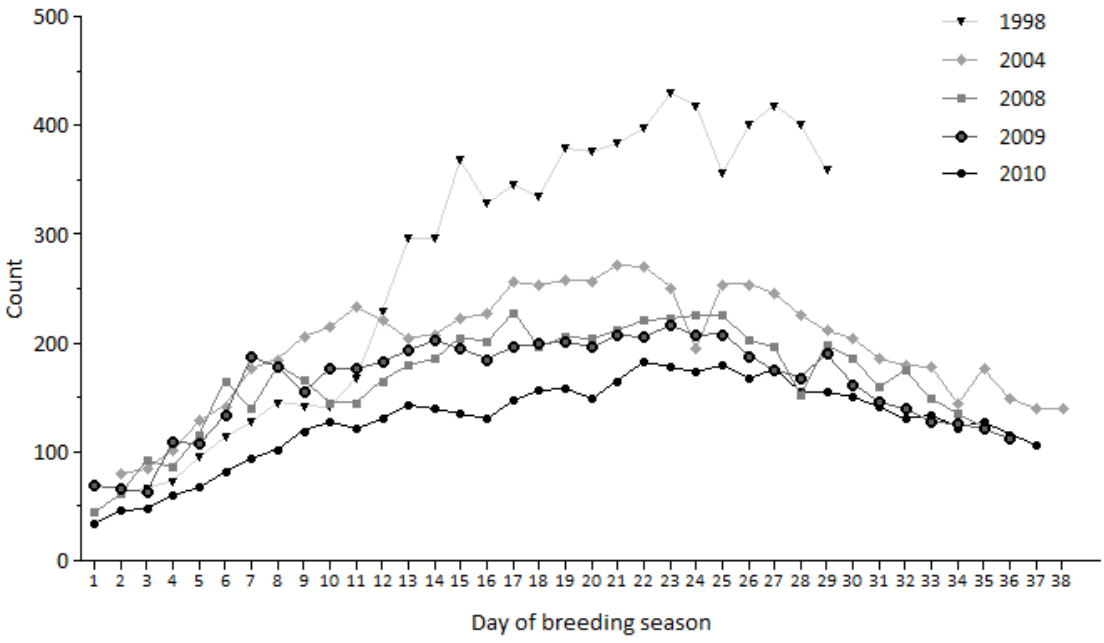


Figure 3.9: Number of adult females ashore on each day of the 1998, 2004, 2008, 2009 and 2010 breeding seasons. In each year, Day 1 = September 28th.

Table 3.6: Measures of female spatial distribution on focal dates relative to other females and to their pups. Mother-pup assignment based on proximity (see Section 2.4.4); SD = Standard Deviation.

Year	Stage of breeding season	Nearest Neighbour Distance (m)		Mother-pup distance (m)	
		Mean	SD	Mean	SD
1998	Early	3.99	2.88	3.80	5.20
	Middle	4.79	2.63	3.90	6.59
	Late	5.19	3.18	2.92	1.71
2004	Early	4.23	3.83	3.84	3.81
	Middle	5.10	3.82	3.30	2.11
	Late	5.97	4.26	3.00	1.59
2008	Early	4.39	3.75	3.51	2.52
	Middle	5.32	5.24	2.93	2.03
	Late	7.72	7.37	3.31	4.10
2009	Late	6.21	4.66	3.22	2.55
	End	8.80	7.56	3.30	3.29
2010	Beginning	4.81	4.27	2.86	1.61
	Middle	5.61	5.15	4.23	4.95
	Late	5.89	6.05	3.55	2.64
	End	9.26	6.74	3.16	2.42

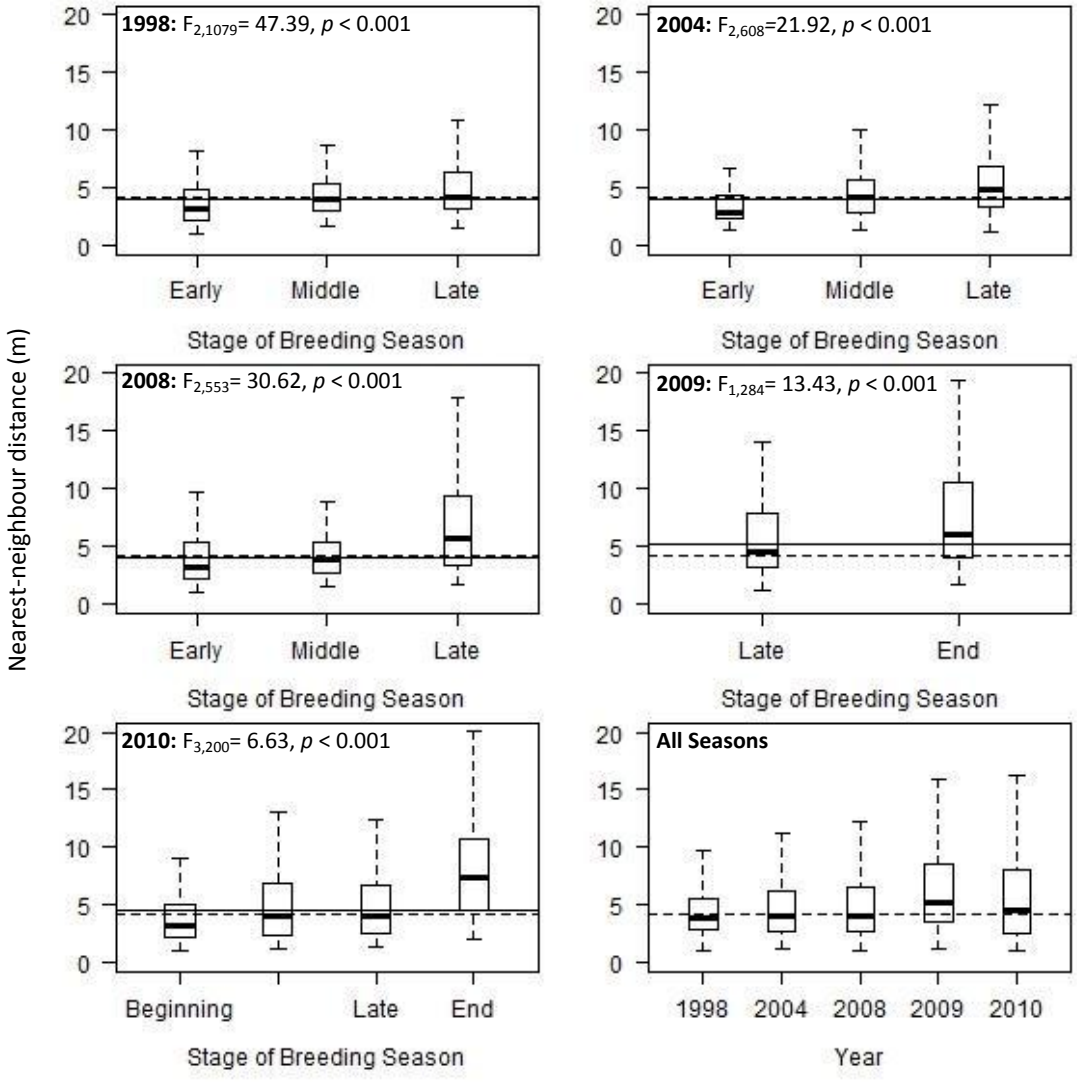


Figure 3.10: Summary of female nearest-neighbour distances on focal dates for each breeding season. The solid horizontal line represents the median nearest-neighbour distance for the focal year. 'Outliers' removed for clarity, though represent real nearest-neighbour distances calculated within the GIS.

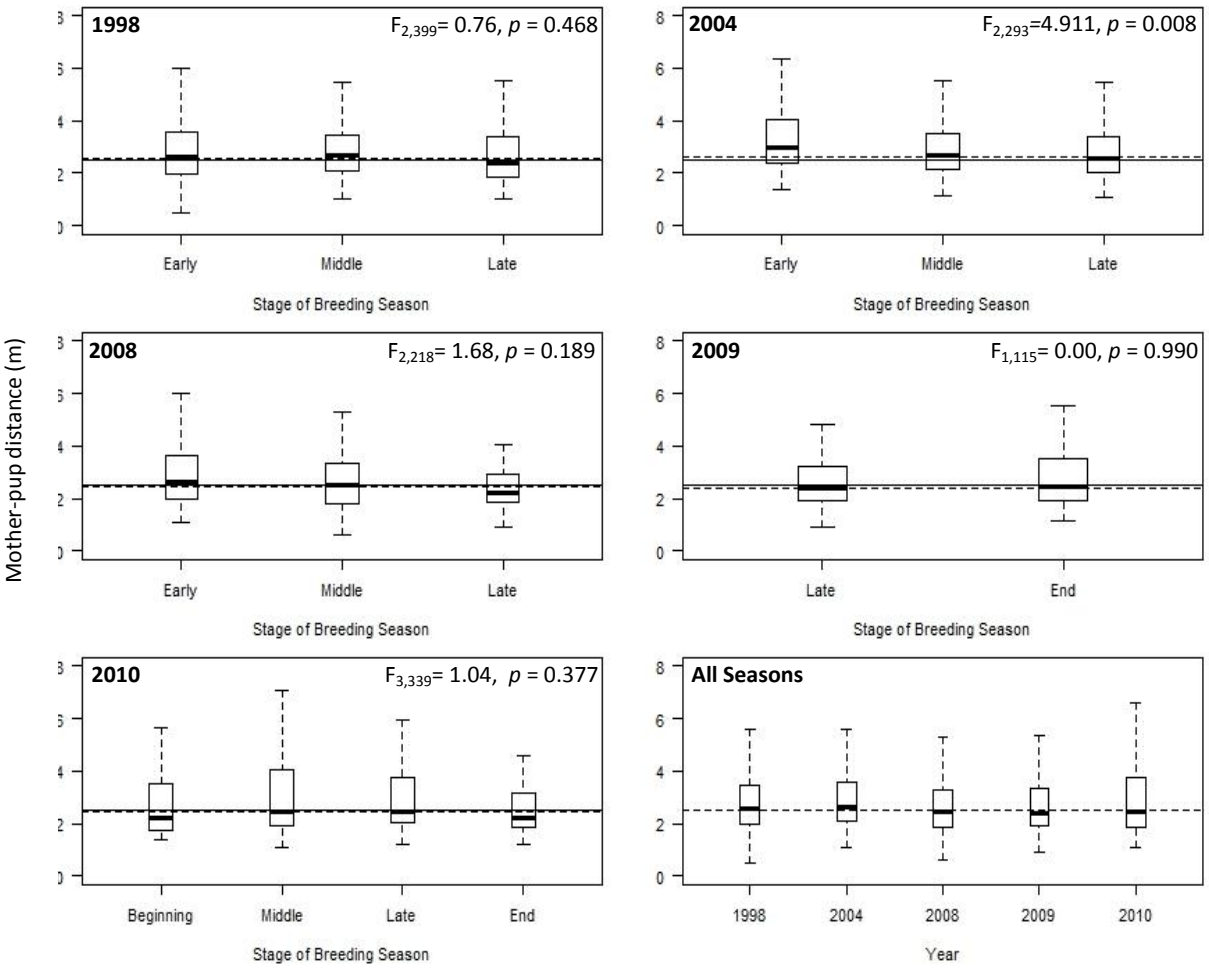


Figure 3.11: Summary of mother-pup distances on focal dates for each breeding season. For each figure, the dashed horizontal line represents the median mother-pup distance over all years and the solid horizontal line represents the median mother-pup distance for the focal year. 'Outliers' removed for clarity, though 'outliers' represent real mother-pup distances calculated within the GIS.

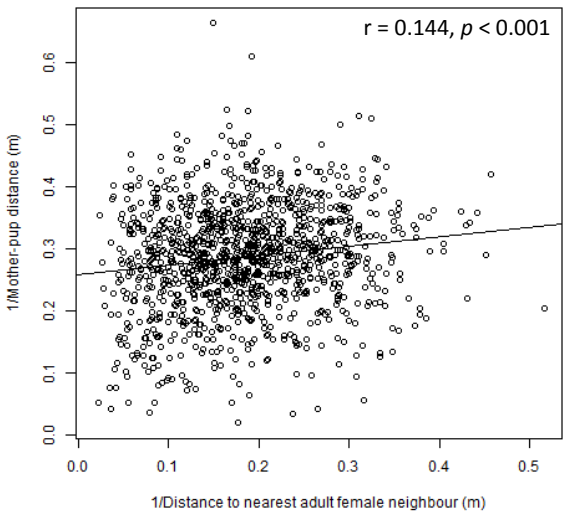


Figure 3.12: (Negligible) positive correlation between mother-pup distance (m) and distance to nearest female neighbour (m) for *individuals* (i.e. each point indicates the mother-pup distance and nearest-neighbour distance of an individual) across all stages of all five breeding seasons, as indicated by Pearson's product-moment correlation. Data shown have been inverse transformed prior to correlation.

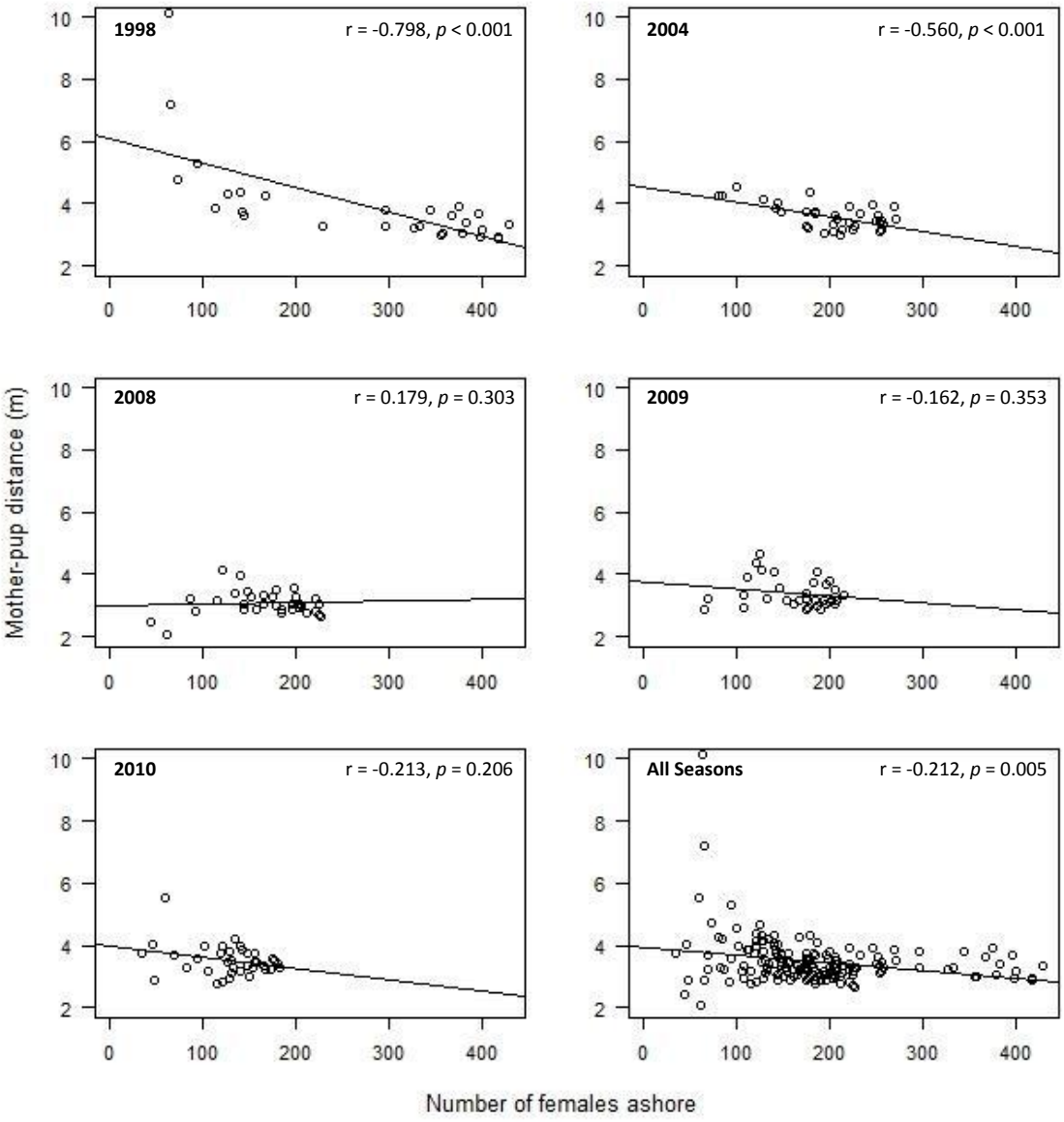


Figure 3.13: Relationship between mother-pup distance (m) and number of females ashore in all years. Pearson's product-moment correlation indicates a significant negative correlation in 1998 and 2004 only, taking into account only the daily means.

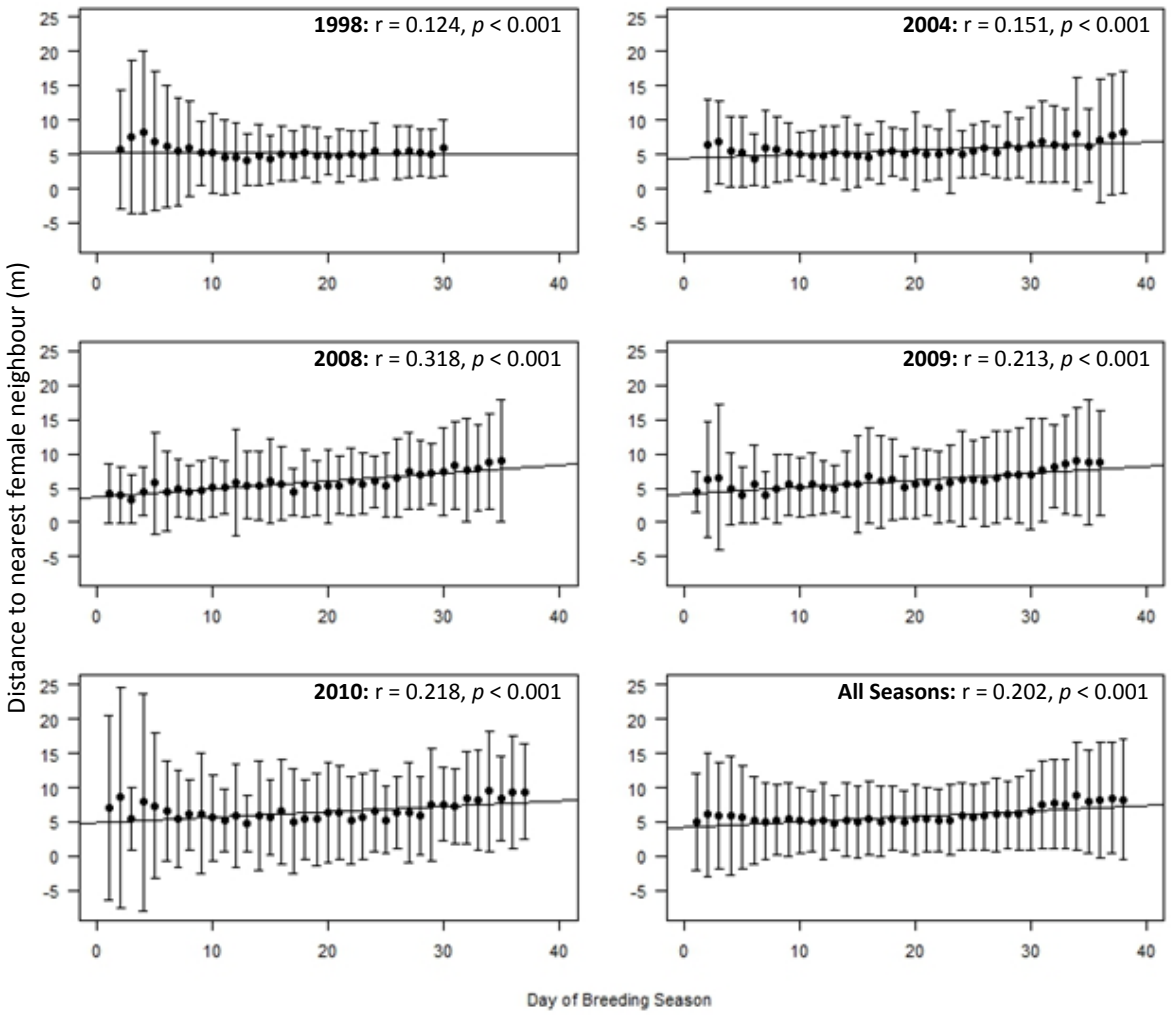


Figure 3.14: Change in distance to nearest female neighbour (m) over every day in all five breeding seasons. In all years, Day 1 = 28th September. Pearson's product-moment correlation indicates a significant positive correlation in all cases, taking into account only the daily means.

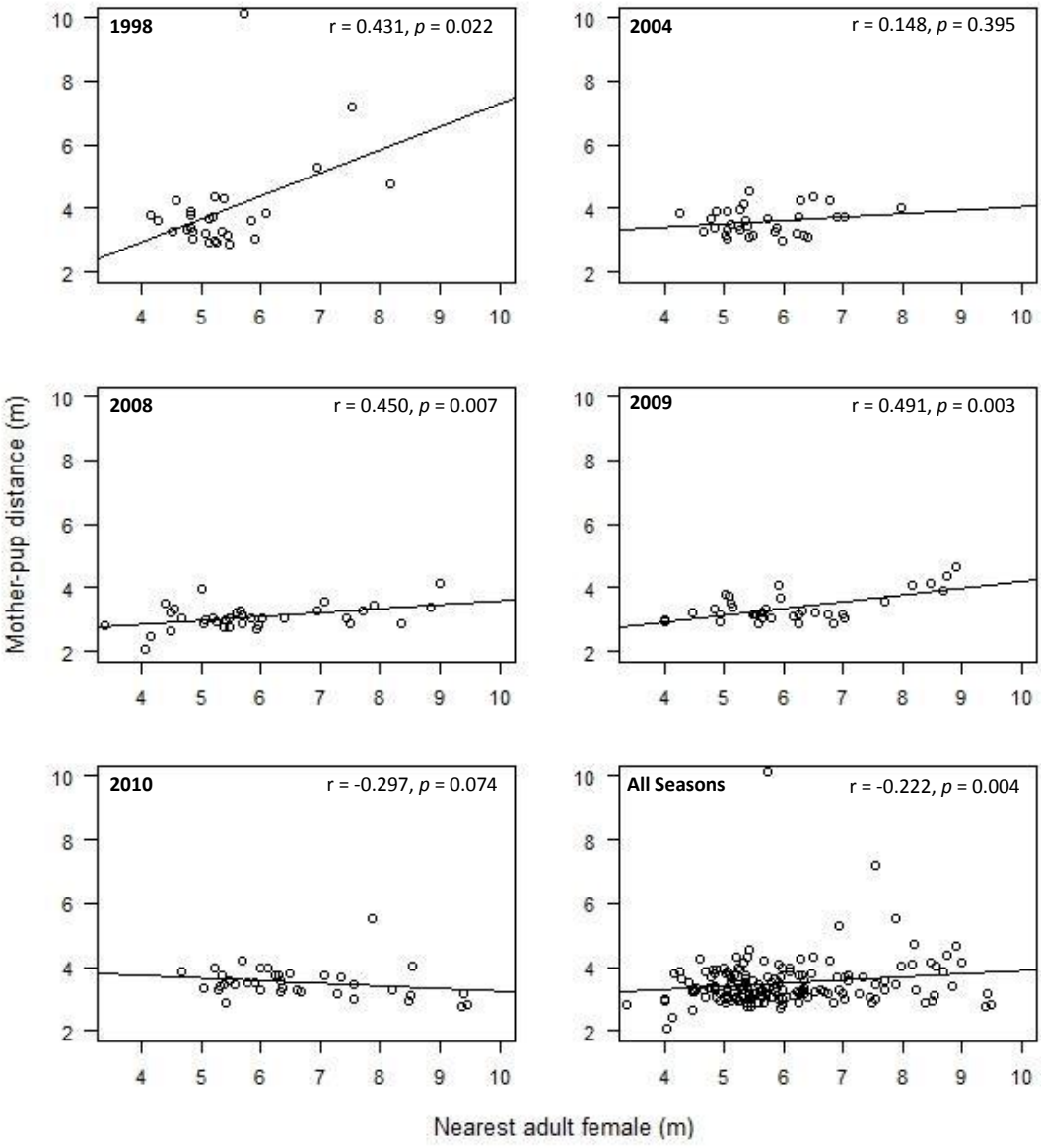


Figure 3.15: Relationship between mother-pup distance (m) and nearest-neighbour distance (m) in all years. Pearson's product-moment correlation indicates that generally mother-pup distance increases with nearest-neighbour distance, taking into account only the daily means.

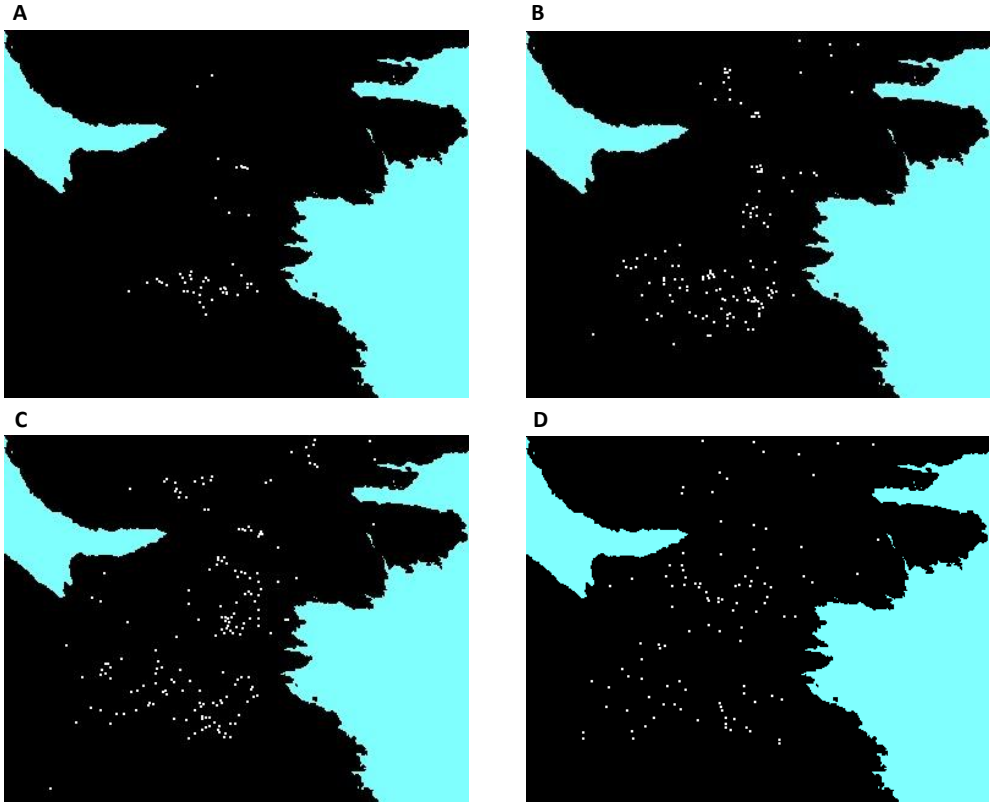


Figure 3.16: Change in distribution of adult female grey seals across the SS on 2010 focal dates, indicated by white points. Points have been enlarged (×4) for clarity; in reality the locations are recorded at a finer spatial scale. **A:** 30/09/2010; **B:** 12/10/2010; **C:** 24/10/2010; **D:** 03/11/2010.

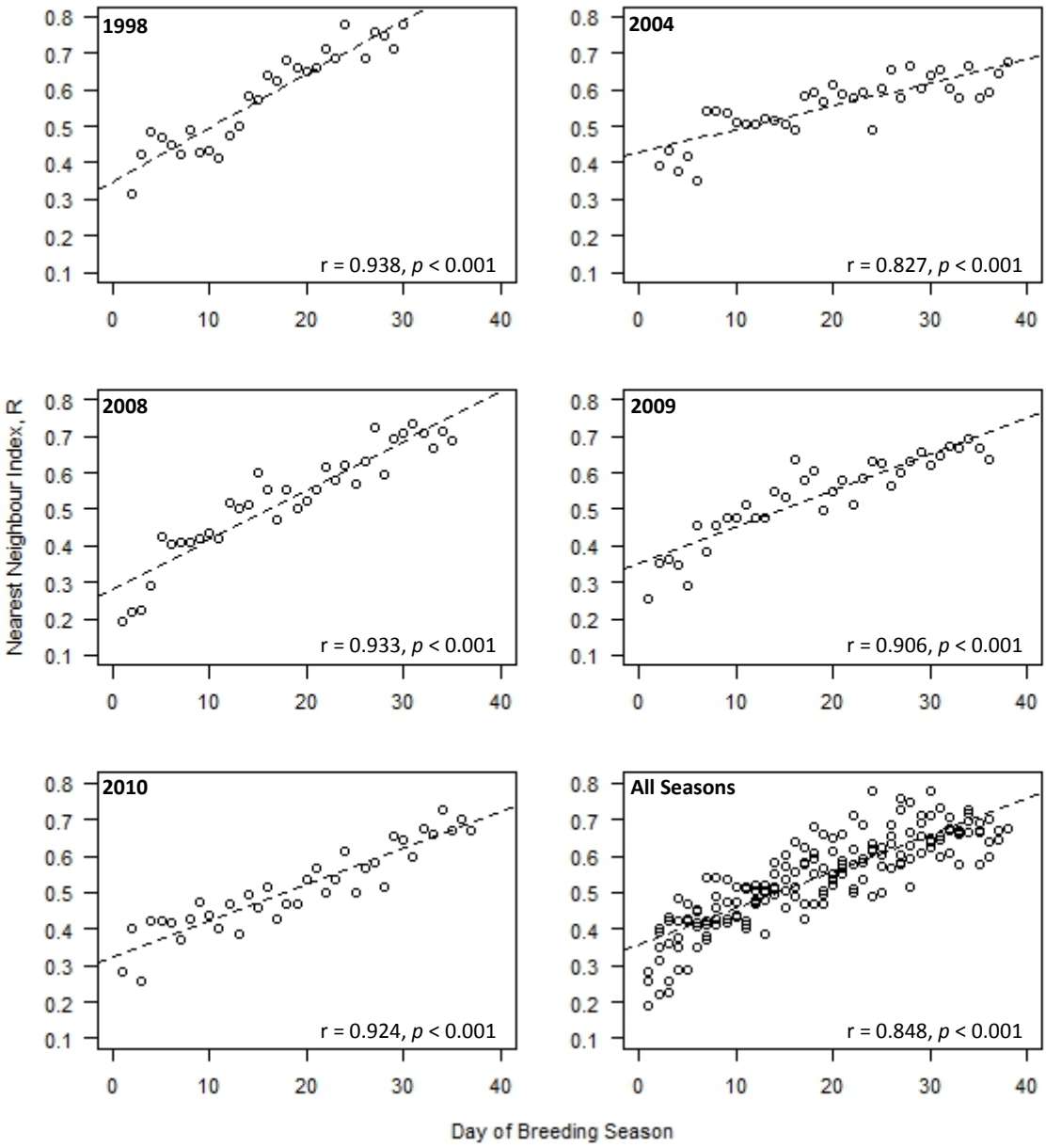


Figure 3.17: Change in nearest neighbour index (*R*) over every day in all five breeding seasons. In all years, Day 1 = 28th September. Pearson's product-moment correlation indicates a significant positive correlation in all cases. Low values of *R* indicate more random dispersion, higher values indicate a more clustered geographic distribution.

Table 3.7: GLM results outlining factors influencing daily nearest neighbour index, *R*; showing Δ-AIC values for all models with Δ-AIC ≤ 6. Those models deemed to be the best (most parsimonious) are highlighted in bold, and are presented alongside the coefficient estimates, with an indication of the associated p-values.

Year	Model[†]	df	Δ-AIC	D Estimate[‡]	C Estimate[‡]	Intercept Estimate[‡]
1998	DC	4	0.000	-	-	-
1998	DCM	5	0.745	-	-	-
1998	DAC	5	1.912	-	-	-
1998	DM	4	1.990	-	-	-
1998	**D**	**3**	**2.050**	**0.015*****	**NA**	**0.019*****
1998	DAM	5	2.270	-	-	-
1998	DACM	6	2.314	-	-	-
1998	DA	4	3.109	-	-	-
2004	DC	4	0	**0.006*****	**<0.001*****	**0.341*****
2004	DCM	5	0.333	-	-	-
2004	DAC	5	1.952	-	-	-
2004	DACM	6	2.172	-	-	-
2008	**DC**	**4**	**0**	**0.012*****	**<0.001****	**0.196*****
2008	DCM	5	1.821	-	-	-
2008	DAC	5	1.846	-	-	-
2008	DACM	6	3.605	-	-	-
2009	DAC	5	0	-	-	-
2009	DACM	6	1.935	-	-	-
2009	**DC**	**4**	**2.707**	**0.009*****	**<0.001****	**0.266*****
2009	DCM	5	4.654	-	-	-
2010	DM	4	0	-	-	-
2010	DAM	5	1.797	-	-	-
2010	DCM	5	2	-	-	-
2010	**D**	**3**	**3.665**	**0.010*****	**NA**	**0.323*****
2010	DACM	6	3.779	-	-	-
2010	DA	4	3.943	-	-	-
2010	DC	4	4.157	-	-	-
2010	DAC	5	5.390	-	-	-

[†] A = Air temperature, C = Count, D = Day of breeding season, M = MSLP.
[‡] Number of asterisks denotes magnitude of p-value (* = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$).

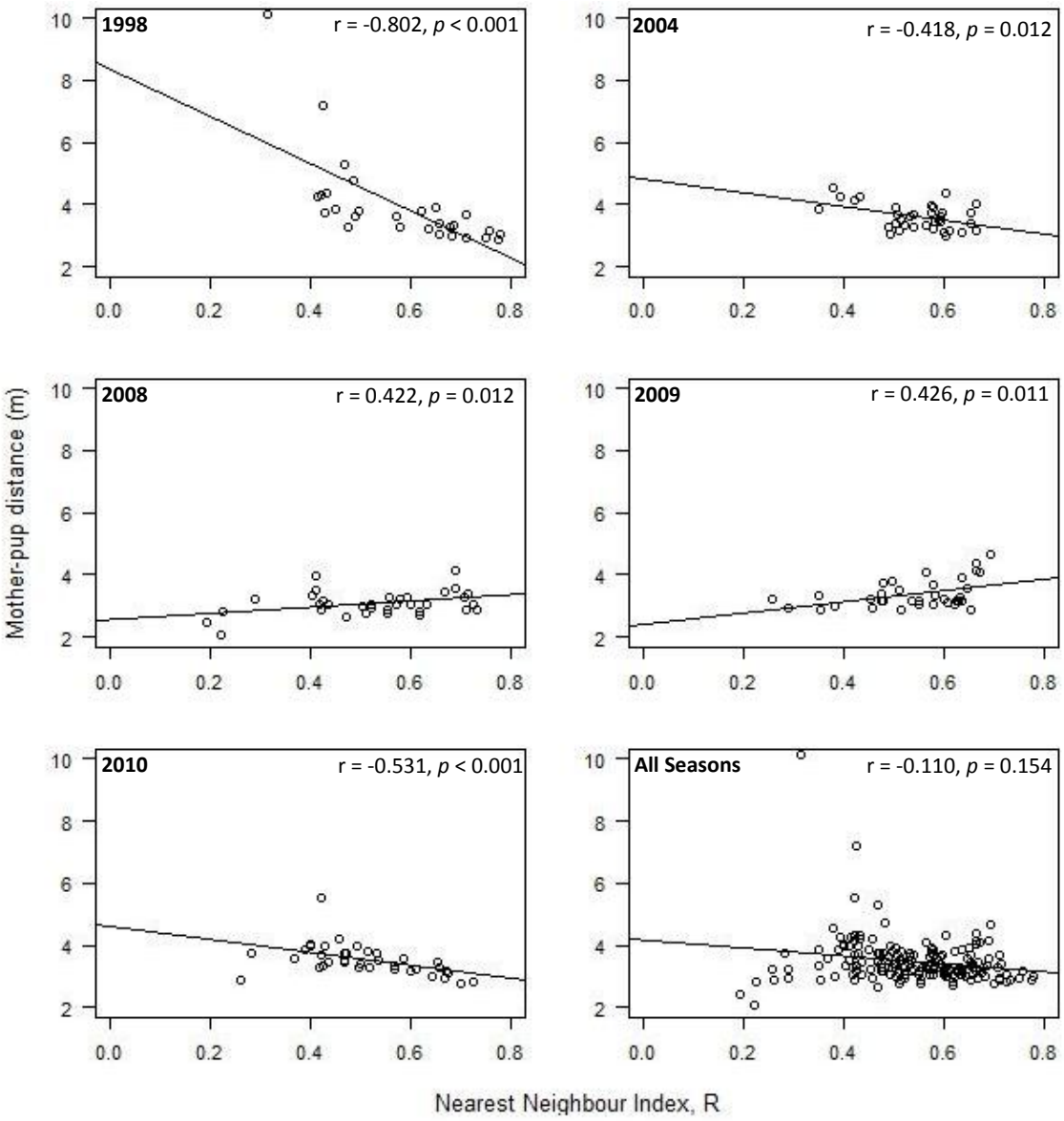


Figure 3.18: Inconsistent relationship between mother-pup distance (m) and nearest neighbour index (*R*) all five breeding seasons. Pearson's product-moment correlation indicates a significant correlation in all individual seasons.

3.3.4 Habitat associations of grey seal females and neonates

3.3.4.1 Elevation

On average, females and neonates tend to occupy sites at elevations close to the mean for the SS: 15.76m (± 8.07m; SD) and 16.88m (± 8.38m; SD) above sea level, respectively (Table 3.8). Overall, this difference between females and neonates is significant (Mann-Whitney U; U = 1811183, p <0.001) though Mann-Whitney U tests performed on individual breeding season stages within each breeding season indicate that neonates are only found at significantly higher elevations than females in the early and mid stages of 1998 and the early and late stages of 2008 (MWU; **Early 1998:** U = 13653.0, p = 0.043; **Mid 1998:**U =32577.5 , p = 0.026; **Early 2008:** U = 3035.0, p < 0.001; **Late 2008:** U = 4581, p = 0.006). In addition, there is considerable variation around the female and neonate means, with significant differences in female elevation values between breeding season stages within the 1998, 2004 and 2008 breeding seasons (Figure 3.19;

Appendix 2, Section A2.4.1); within these seasons, where there are significant changes in elevation used, the average elevation of female locations increases as the season progresses, as females move inland towards higher ground (Appendix 2, Section A2.4.1). The same is true of neonate locations, which increased over the season in 2004 and 2008; however in 2004, females and neonates were found at higher elevation in the middle of the breeding season rather than at the end (Figure 3.19; Appendix 2, Section A2.4.1).

Table 3.8: Means and standard deviations (SD) of the seal elevation values (m). The global distribution of elevation is consistent throughout all years (mean = 17.39 ± 12.09m (SD)).

Year	Period	Females		Neonates	
		Mean	SD	Mean	SD
1998	Early	13.59	8.34	15.27	9.48
	Middle	15.31	8.84	16.83	9.84
	Late	17.51	10.45	17.68	9.36
2004	Early	15.18	6.98	16.92	8.10
	Middle	17.23	7.88	18.06	8.30
	Late	15.57	6.85	15.55	6.97
2008	Early	13.14	5.68	16.40	6.29
	Middle	16.32	6.70	17.59	6.76
	Late	16.82	8.55	20.63	10.97
2009	Late	17.01	7.62	16.70	7.92
	End	16.39	7.67	15.84	8.49
2010	Beginning	13.83	3.93	14.55	3.25
	Middle	14.93	5.83	15.21	5.87
	Late	14.84	6.60	16.11	7.03
	End	16.37	7.04	17.29	6.64
Mean		15.60	-	16.71	-

The distribution of females relative to other seals does not appear to be linked to the elevation at which they are found: there was a significant, negligible positive correlation between female elevation and both NNdis and MPdis (Appendix 2: Section A2.4.1, Figures A2.11 - A2.12).

3.3.4.2 Cost-distance to nearest access

On average, females and neonates occupy sites with relatively low CACC (Table 3.9, Figure 3.20): their mean CACC values are 28.05 (± 15.25; SD) and 30.27 (± 15.55; SD), respectively. Overall, the difference between females and neonates is significant (Mann-Whitney U; U = 1825534, p<0.001) though Mann-Whitney U tests performed on individual breeding season stages within each season indicate that neonates are only found significantly further from access than females in the early and mid stages of 1998 and the early and late stages of 2008 (MWU; **Early 1998:** U = 13621.0, p = 0.040; **Mid 1998:**U =33061.0 , p = 0.049; **Early 2008:** U = 3201.0, p < 0.001; **Late 2008:** U = 4640, p = 0.008). This is to be expected given the female and neonate distribution relative to the elevation across the SS, as elevation is important in creating the CACC surface.

In addition, there is considerable variation around the female and neonate means, with significant differences in female CACC values between breeding season stages within all breeding

seasons except 2009 (Table 3.9; Appendix 2, Section A2.4.2). Where there are significant changes in CACC within a breeding season, the average CACC of female locations increases as the season increases; in other words, females move further inland, away from access points, as the season progresses (Appendix 2, Section A2.4.2). The same was true for neonates, which showed significant differences in within-season CACC values in 1998, 2004 and 2008. Similarly to the females, where there are significant changes in CACC over a breeding season, the average CACC of neonate locations generally increases as the season progresses (Appendix 2, Section A2.4.2). The 2004 breeding season was the only exception to these trends for both females and neonates, which were found at further inland in the middle of the breeding season.

The distribution of females relative to one another (NNdis) does not appear to be linked to the CACC value of locations at which they are found: there was a negligible positive correlation between female CACC and NNdis and no correlation between CACC and MPdis (Appendix 2, Section 2.4.2; Figures A2.14 and A2.15).

Table 3.9: Means and standard deviations (SD) of the seal 'cost-distance' to access (CACC) values. The global distribution of CACC is consistent throughout all years (mean = 31.64 ± 22.36m (SD)).

Year	Period	Females		Neonates	
		Mean	SD	Mean	SD
1998	Early	23.75	15.62	26.82	17.21
	Middle	27.19	16.39	29.86	17.38
	Late	31.10	18.39	31.93	16.65
2004	Early	26.03	13.28	29.18	14.83
	Middle	30.77	14.83	32.56	15.51
	Late	28.55	13.98	28.24	13.99
2008	Early	22.78	12.07	29.38	13.08
	Middle	29.27	13.30	31.80	12.70
	Late	30.93	16.05	37.79	18.58
2009	Late	30.54	14.80	30.01	15.13
	End	29.90	14.95	29.34	16.82
2010	Beginning	23.20	7.93	24.74	6.39
	Middle	26.07	11.74	26.31	12.20
	Late	25.95	13.22	28.76	14.66
	End	30.37	13.70	32.83	12.41
Mean		27.76	-	29.97	-

3.3.4.3 Cost-distance to nearest pool

On average, females and neonates tend to occupy sites with relatively low CPOOL (Table 3.4, Figure 3.21): 7.49 (± 7.64; SD) and 7.73 (± 7.56; SD), respectively. Overall, this difference is not significant (Mann-Whitney U; U = 1952578, p = 0.104). However, comparisons of individual focal days indicate that, where there are significant differences in CPOOL values, neonates are found further from pools than females (Figure 3.21). This occurs in the early and mid stages of 2004 and the end of both the 2009 and 2010 seasons (MWU; **Early 2004:** U = 3367.0, p = 0.019; **Mid 2004:**U =17200.0 , p = 0.007; **End 2009:** U = 2389.0, p = 0.029; **End 2010:** U = 1504.5, p = 0.0420).

In addition, there is considerable variation around the female and neonate means, with significant differences in female CPOOL values between breeding season stages within all breeding seasons (Table 3.4; Appendix 2, Section A2.4.3). Where there are significant changes in CPOOL values used within a breeding season, females are further from pools of water as the season progresses (Appendix 2, Section A2.4.3). There were also significant differences in within-season CPOOL values at neonate location in 1998, 2004 and 2008 (Table 3.4; Appendix 2, Section 2.4). Similarly to females, neonates are typically found further from pools later in the season than earlier in the season (Appendix 2, Section A2.4.3). There are a number of exceptions to this trend for both females and neonates: in 1998, females and neonates were found closer to pools in the middle of the breeding season than early or late in the season, whilst in 2008 females were found closer to pools in the middle of the season than early in the season. Finally, both females and neonates were found significantly closer to pools at the end of 2009 than in late 2009. This is unsurprising given the increased availability of pools in these stages of the breeding season (Section 3.3.1.3) and the generally warmer weather later in the season, which may necessitate adult female proximity to pools for thermoregulation.

The distribution of females relative to other individuals does not appear to be linked to the CPOOL value of locations at which they are found: there was a significant though negligible positive correlation between female CPOOL and NNdis and no correlation between female MPdis and CPOOL at sites occupied by females (Appendix 2, Section 2.4.3; Figures A2.17 and A2.18).

3.3.4.4 Salinity

On average, females and neonates tend to occupy sites with very low salinity (Table 3.5, Figure 3.22): 0.80‰ (± 1.16; SD) and 0.75 ‰ (± 1.10; SD), respectively; overall, this difference is significant (Mann-Whitney U; U = 1903042, p = 0.003). However, comparisons of individual focal days indicate that neonates are found at sites of lower salinity than females only in mid and late 2004 and mid 2008 (MWU; **Mid 2004:** U = 13319.0, $p < 0.001$; **Late 2004:** U =8917.0 , $p < 0.001$; **Mid 2008:** U = 8906.0, $p < 0.001$).

There are significant differences in female salinity values between breeding season stages within all breeding seasons except 2009 (Table 3.5; Appendix 2, Section 2.4.4). Where there are significant changes in salinity within a breeding season females are typically found in areas of higher salinity as the season progresses (Figure 3.22). The same was true for neonates, which showed significant differences in within-season salinity values in 1998 and 2010 (Table 3.5; Appendix 2, Section 2.4.4) and were typically found at sites of higher salinity later in the season. Though not statistically significant, this is a trend which can be seen in all other seasons for both females and neonates (Figure 3.22).

The distribution of females relative to other individuals does not appear to be strongly linked to the salinity value of locations at which they are found: there is a negligible positive correlation between female salinity and NNdis and no significant correlation between female MPdis and the salinity at the site occupied by females. In other words, there was a slight tendency for females at higher salinity sites to be further from their nearest adult female neighbour, but not their pups (Appendix 2, Section A2.4.4; Figures A2.20 and A2.21).

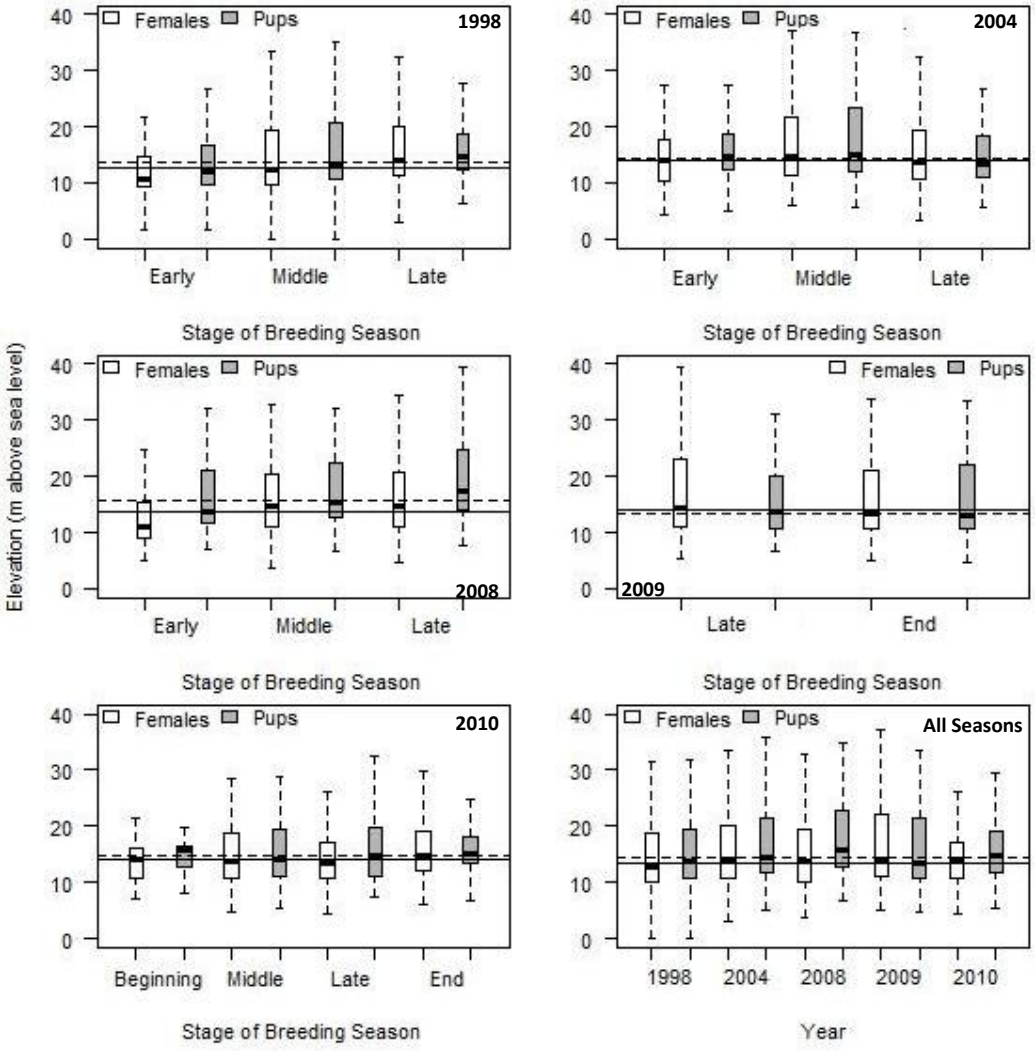


Figure 3.19: Elevation of female and neonate locations during each focal day and breeding season. For each season, the horizontal dashed line represents the neonate median and the solid horizontal line represents the female median. Outliers removed for clarity; see Appendix 2, Figure A2.10 for a corresponding boxplot

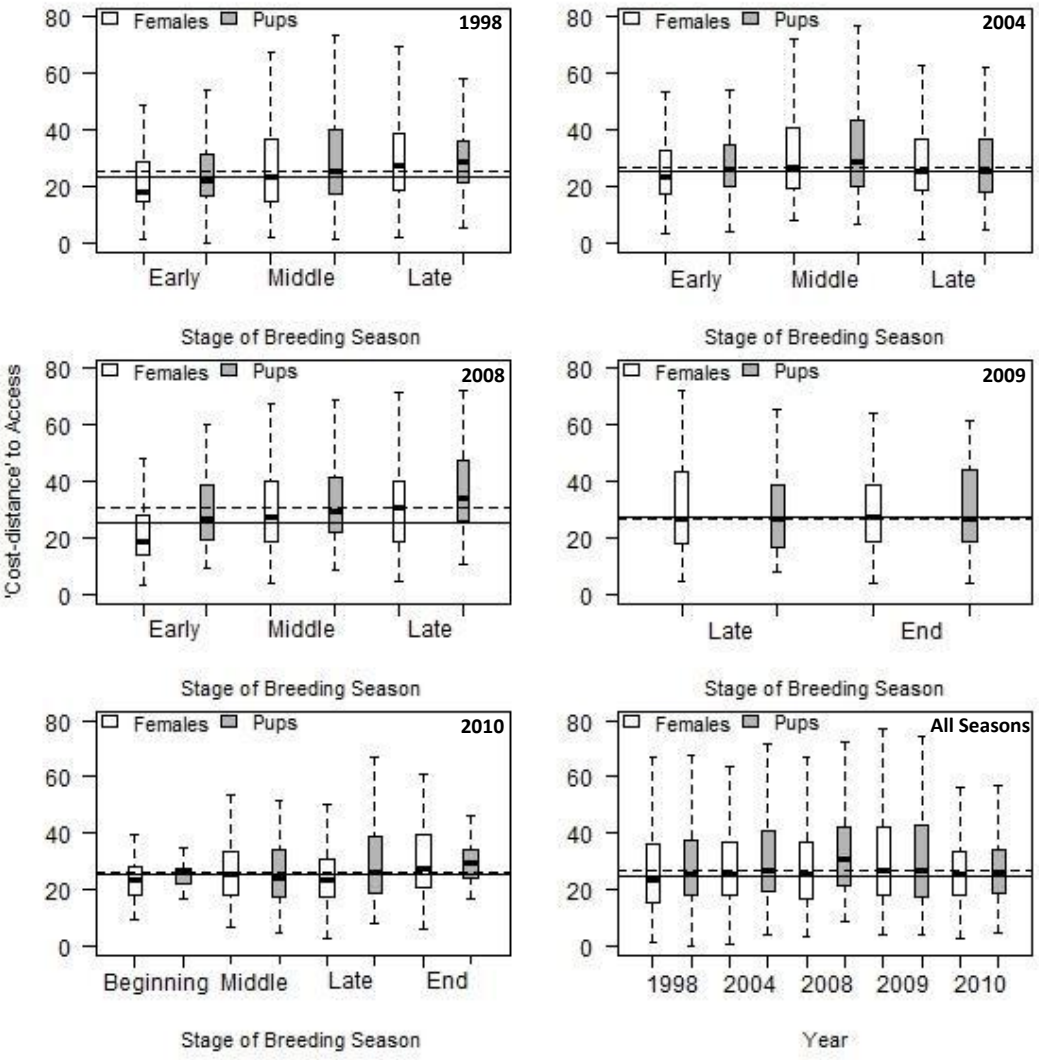


Figure 3.20: 'Cost-distance' to access of female and neonate locations during each focal day and breeding season. On all graphs the horizontal dashed line represents the neonate median over the season and the solid horizontal line represents the female median. Outliers removed for clarity; see Appendix 2, Figure A2.13 for a corresponding boxplot containing the outliers.

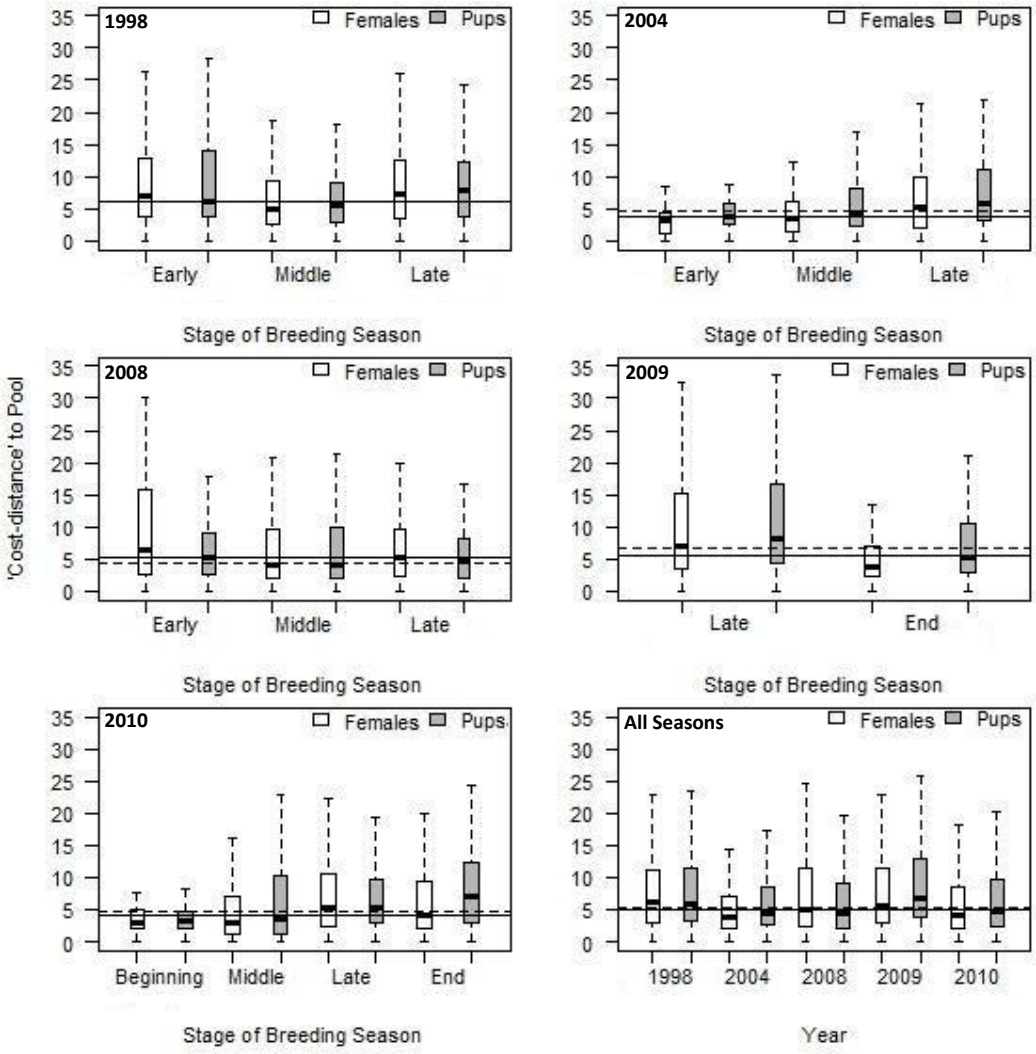


Figure 3.21: 'Cost-distance' to nearest pool of female and neonate locations during each focal day and breeding season. On all graphs the horizontal dashed line represents the neonate median over the season and the solid horizontal line represents the female median. Outliers removed for clarity; see Appendix 2, Figure A2.16 for a corresponding boxplot containing the outliers.

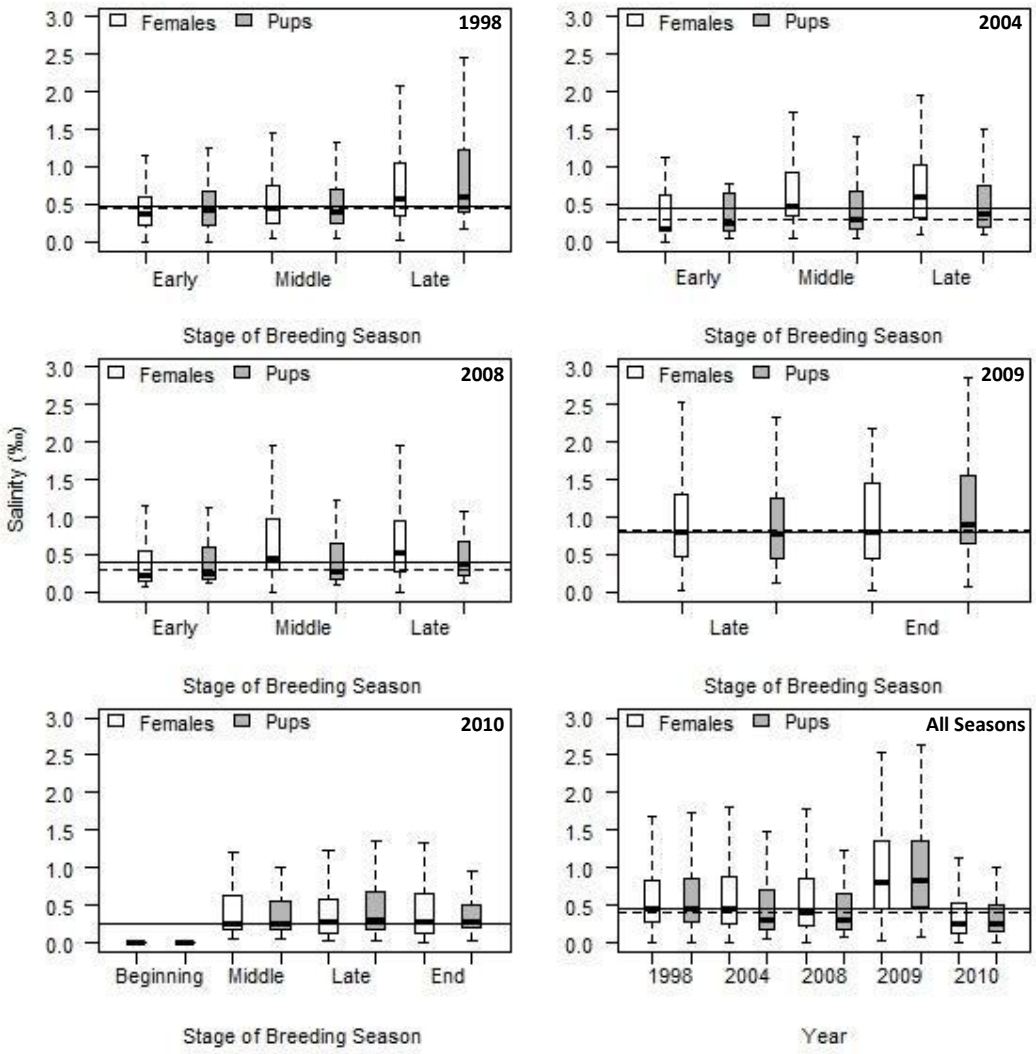


Figure 3.22: Salinity (‰) of female and neonate locations during each focal day and breeding season. On all graphs the horizontal dashed line represents the neonate median over the season and the solid horizontal line represents the female median. Outliers removed for clarity; see Appendix 2, Figure A2.19 for a corresponding boxplot containing the outliers.

3.4 Discussion

This chapter has analysed the habitat and distribution of grey seals on North Rona at a scale relevant to the individual seal. In doing so, it has revealed that the SS is spatially heterogeneous in terms of all four EGVs measured, with a broad range of each EGV across the SS. In addition, the SS is temporally heterogeneous in terms of the distribution of cost-distance to pool and salinity, which change significantly across the relatively short timescale of a breeding season. It was also revealed that females colonising North Rona at the beginning of each season remain relatively clustered relative to one another, and become more randomly dispersed as the season progresses. During their time ashore, females tend to occupy sites with low values in a restricted range of each EGV. This indicates that individuals may be exhibiting a preference; Chapter 4 will explore potential site preferences further, examining site use in relation to the 'global' availability of each EGV. Furthermore, the EGV values at sites occupied by females are

similar to those at sites occupied by neonates, and the trends in change of each EGV used over each season are also similar. This is unsurprising given the consistently short mother-pup distance maintained throughout each season, which is important for pup protection and feeding during the intensive lactation period (Kovacs, 1987; Mellish *et al.,* 1999). Despite the high degree of similarity, the niches of females and neonates will be modelled separately in Chapter 4 in an attempt to distinguish female habitat and pupping site preferences. Based on results presented here it appears that these preferences will differ most in relation to proximity to pools and access points, to which females are typically closer than are neonates.

This chapter has shown that the fine scale habitat at North Rona changes significantly within each breeding season, with generally wetter and more saline conditions over the SS as each season progresses. Integrating the EGV and weather data reveals that, as may be expected, the availability of pools of water (indicated by average CPOOL values) is influenced by daily rainfall: focal days with low average global CPOOL typically follow periods of high rainfall. Unfortunately the quality of the rainfall data means that these inferences must be made cautiously. CPOOL is typically lower, on average, towards the end of each season; however, this trend is reversed in 2004. In 2004, as expected, there was little or no rain on the days prior to collection of CPOOL data. Average pool salinity increases as each season progresses; in general those areas that become most saline are in the north-west of the SS, and in regions around the main access gullies. In the north-west the increase in salinity likely results from increasing sea spray over the season as the weather and sea conditions worsen, whilst increasing salinity around the access gullies may be a result of sea spray and salt washing off of seals as they bathe in or pass through the pools upon arrival at the colony. This change in habitat availability within each season could have important implications for female distribution due to their thermoregulatory requirements and potential need for drinking water; this is of further importance as the distribution of females has implications for, e.g., the degree of sexual selection and sociality amongst grey seals (Twiss *et al.,* 2000a, 2007; Pomeroy *et al.,* 2005), as is discussed in Chapter 6.

The average weather at North Rona does not change significantly between breeding seasons; however, as highlighted above, the intra-annual variability in weather conditions could be key to explaining some trends, for example in the distribution of pools over the SS. The air temperature, which averages approximately 10°C, could also be important in determining female distribution relative to these pools as air temperature will determine their requirements for behavioural thermoregulation. The weather preceding focal days will therefore be considered further in Chapter 4, where it may have a role in explaining trends in female site choice.

Previous studies have noted the increase in population stability often associated with landscape heterogeneity at multiple scales (Piha *et al.,* 2007; Luoto and Heikkinen, 2008; Oliver *et*

al., 2010). Despite fine-scale heterogeneity at North Rona one of the most notable findings here is the overall decrease in the number of individuals ashore between breeding seasons. However, landscape heterogeneity typically contributes to population stability by increasing the availability of different foraging niches. Therefore, landscape heterogeneity may be less important for the grey seal, due to the temporal and spatial separation of breeding and foraging. This chapter supports previous suggestions that the colony is in decline, unlike many others in the Outer Hebrides group (Duck and Morris, 2011; CDD and PPP *unpubl. data*). This population decline does not appear to be related to density-dependent effects of habitat availability, as inter-annual consistency in EGVs indicates little change the availability of a range of habitat types between seasons. Furthermore, there does not appear to be a significant inter-annual difference in the average of any EGVs at sites occupied by females, despite considerable intra-seasonal variability. It is also worth considering that the rapid decline in the number of individuals breeding at North Rona may have given rise to a change in population context, with the removal of the previous constraint of high density. Due to the potentially different population context in recent years compared to 20 years ago, it is possible that there may be changes in aspects of grey seal ecology such as pupping site fidelity, parturition date and movements post-partum, which may previously have been constrained by high breeding densities which limit site choice and movement.

In every year, females become more dispersed as the season progresses; this finding is associated with a small effect size (Figure 3.14) yet supports previous studies, which noted a decline in female aggregation at North Rona over each season (Pomeroy *et al.,* 1994). Despite this trend, it remains clear that adult females are more clustered throughout the season than would be expected by chance. However, contrary to the findings of Pomeroy *et al.* (1994), the degree of aggregation does not appear to decrease in line with increased rainfall; it may be that due to the North Rona population decline females are less aggregated throughout the season than they were 20 years ago, when Pomeroy *et al.* (1994) collected their data, meaning that similar trends in aggregation cannot be identified. Instead the degree of aggregation appears to consistently correlate with the day of the breeding season. This suggests that the increase in dispersal may arise as a result of the turnover of females throughout the season, with newly arriving females colonising new sites, and females that have weaned their pups vacating sites in between these new females. Though females become more dispersed relative to one another over each season, they remain in close proximity to their pups. It may be expected that mother-pup distance should decline over the breeding season as the increasingly mobile pup is better able to actively maintain close proximity to its mother and attempt to initiate suckling bouts; however, this is not apparent in the data presented here. This may be a result of the turnover of females throughout the season, as not all pups will be at the same stage of development and not all will be equally capable of maintaining proximity to their mothers.

Previous studies of female distribution at North Rona have indicated that colonisation of the island follows a similar pattern in all years (Anderson *et al.,* 1975; Pomeroy *et al.,* 1994). Visual inspection of female distribution maps throughout each season indicates that these patterns have been conserved in the intervening years (PPP, *pers. comm.*). As suggested by Anderson *et al.* (1975), the gregarious nature of the grey seal means that it is likely that the first females ashore determine the subsequent site choices of new arrivals; this, combined with the high degree of pupping site fidelity shown by adult females (Pomeroy *et al.,* 1994) is a likely cause for the conservation of colonisation patterns. However, as females are known to select pupping sites based on fine-scale topographical features, this also suggests that it may only be the first few females ashore that get a real choice of pupping site, with preferential colonisation perhaps excluding later females from the more preferred sites. This has implications for out interpretation of models of female site preferences, and will therefore be considered further in Chapter 4.

In addition to noting the consistency in colonisation patterns on North Rona, Pomeroy *et al.* (1994) found that aggregations of females were often associated with access gullies, concluding that local topography is important in determining female dispersion. Subsequent studies also found that females prefer specific habitat features, which limits their space use to areas in close proximity to these access points and to pools of water (Twiss *et al.,* 2000a; 2001; Redman *et al.,* 2001; Twiss *et al.,* 2007). The results presented here corroborate those of previous studies, though it is apparent that females are typically not found directly next to pools or access points, as indicated by female utilisation of sites with intermediate values for these EGVs. This is likely a result of females avoiding those areas which act as thoroughfares for arriving and departing seals (Anderson *et al.,* 1975; Twiss *et al.,* 2001). In addition to confirming the results of previous studies, the results presented in this chapter also show that females and neonates are typically not found in the areas of highest salinity; this is intriguing given previous observations of females drinking from pools of water and suggests that females may choose sites of low salinity based on preferences for the salinity of their drinking water. Females are found close to pools throughout all breeding seasons, despite an increase in average pool salinity due to, for example, sea spray; it may be that though pools become less suitable for drinking over the season they are still important for thermoregulation. One of the more interesting differences between female and neonate locations is that neonates tended to be found in less saline areas than females. Although this difference was statistically significant, it seems unlikely that it is *biologically* significant. The differences in salinity at female and neonate locations are vanishingly small (0.05‰ on average), and it seems unlikely that seals could distinguish this difference based solely on taste (Friedl *et al.,* 1990); this is discussed further in Section 4.4. Furthermore, this difference may simply be an artefact of how the salinity surface was interpolated and could thus be explained by female and neonate proximity to the nearest pool of water. Due to the nature of point interpolation, it is

probable that sites close to pools containing saline water are classed as slightly more saline than sites further from pools; as neonates were typically further from pools than females were, this could explain the apparent difference in salinity at female and neonate sites. Despite this problem with the salinity surfaces, salinity will be retained for further analyses. This seems reasonable as the small differences such as those between female and neonate sites represent only a small fraction of the range of salinity values available over the SS; it appears that individuals typically avoid the more brackish pools, which are of such high salinity that it may be reasonably expected that one could discriminate between these and freshwater pools, with a choice between such pools possibly being important in the site choice decisions of the early colonisers.

The EGV values at occupied sites change within each season, typically in explicable ways; however, there are a number of changes within each season (identified above) that do not seem to fit any trends. It is important to note however that this method of comparing EGV use by females does not take into account habitat use *relative* to that which is available over the SS as a whole, which may help to explain some of these changes. For example, females and neonates are found closer to pools at the end of 2009 than slightly earlier in the season; this may be a result of an increase in number and area of pools, as indicated by the lower average global CPOOL at this point in the season. This chapter has described the immediate environment of the grey seals at North Rona, and how their use of it has changed over and between five breeding seasons. On the basis of these descriptions it has been possible to identify potential site preferences, given the restricted range of EGVs at sites occupied by seals. However, it is clear that site use needs to be considered relative to habitat availability. Chapter 4 will build on this using niche models to elucidate the potential habitat and pupping site preferences of adult females relative to these EGVs.

4. Habitat and Pupping Site Preferences of Female Grey Seals

4.1 Introduction

Chapter 3 showed that grey seals at North Rona are faced with a heterogeneous landscape with spatially and temporally variable resource distributions. It is expected that, in such a situation, individuals will make their site choice decisions based on the various fitness costs and benefits presented by the range of sites, and that these choices will therefore be subject to natural selection (Partridge, 1978). Grey seals only occur at sites on North Rona within a restricted range of elevation, proximity to access, proximity to pool and salinity, suggesting an element of 'choosiness' amongst the available range of conditions. The aim of this chapter is to reveal the influence of each of these EGVs on seal distribution, and attempt to distinguish between habitat and pupping site selection. These EGVs are thought to have a direct effect on individual distribution (sections 2.2.2 and 4.1.3), with costs and benefits associated with thermoregulation, locomotory costs, mother-pup proximity and maintenance of a positive water balance (Twiss *et al.,* 2000a, 2001, 2002, 2003; Redman *et al.,* 2001), which combined likely influence individual fitness. Natural selection on these fitness effects will likely result in active choice of sites with greater overall benefits, rather than individuals settling in the first available site.

This chapter uses ecological niche modelling to reveal habitat and pupping site preferences of female grey seals in relation to these EGVs, essentially comparing the EGVs at seal locations with the global EGV availability to establish female preferences. This is achieved using the fine-scale location and EGV data in the GIS database described in Section 2.4. In summary, this GIS contains daily, meter-accurate locations of all seals in addition to topographical information on the study area, including slope, elevation, land extent and pool distribution and salinity data. The scale of these data, and the analytical techniques afforded by GIS technology, facilitate a more quantitative approach to defining habitat preferences than has previously been accomplished (Anderson and Harwood, 1985; Pomeroy *et al.,* 1994; Twiss *et al.,* 2000a), allowing integration of knowledge regarding the spatially and temporally heterogeneous distribution of resources and individuals within an accurate representation of the SS at North Rona.

4.1.1 Species Distribution Modelling approaches: an introduction

As outlined in Section 1.4, there is now a whole host of multivariate statistical approaches available which operate alongside a GIS to define habitat preferences and predict species distributions based on the data available here. Most common techniques rely on the use of PA data (e.g. logistic regression or classification and regression trees; Guisan and Zimmerman, 2000; Segurado and Araújo, 2004). However, the nature of the grey seal distribution data available here requires that this study utilises a form of PO SDM technique, excluding the use of popular

techniques such as GLMs and GAMs, which require PA data (Guisan and Zimmerman, 2000). Technically the seal presence data is open to interpretation as PA data, by utilising presences and randomly generated pseudo-absences, as recommended by a number of studies (Osborne *et al.,* 2001; Stockwell and Peterson, 2002). However, it has previously been advised that the use of pseudo-absences may introduce a bias to the data in cases where the species is widespread or presence points are few (Boyce *et al.,* 2002). Furthermore, PA approaches are susceptible to the effects of 'false absences'. Seals may be absent from an area for one of three reasons: (i) failure of detection during surveying, despite seal presence (Kéry, 2002) (ii) absence in suitable areas due to historical reasons including, but not limited to, colonisation patterns and dispersal (Svenning and Skov, 2004) (iii) absence due to the unsuitable nature of the habitat; this latter situation is the only case of a 'true' absence that is valid for basing PA SDM predictions on. The first of these causes of apparent absence seems unlikely for the grey seal at North Rona due to the extensiveness of the surveys performed from an ideal observation vantage point (Section 2.4.2) and the ease of locating all seals on the relatively open, refuge-free topography of North Rona. However, the second cause may lead to erroneous conclusions being drawn regarding HS at particular locations on North Rona; this is because the colony is in decline (Smout *et al.,* 2009; Duck and Morris, 2011; CDD and PPP, *unpubl. data*; Section 3.3.3) and, therefore, fewer sites will be in use in later years than in earlier years. Consequently, not all suitable sites will be in use and some may be wrongly classified as unsuitable. In addition, it has been argued that PO approaches are more useful than PA approaches for describing the fundamental niche (Zaniewski *et al.* 2002) and should, therefore, be preferred despite the concerns raised by Brotons *et al.* (2004) regarding 'optimistic' suitability predictions often made by PO approaches. Therefore this study uses ENFA, a PO modelling framework, to describe the grey seal niche.

4.1.2 Ecological Niche Factor Analysis

ENFA requires just PO data and a set of environmental descriptors (EGVs) to assess habitat preferences and compute HS by comparing the species' distribution on the EGVs (i.e. the values of EGVs at locations with seals present) with the global set of EGV values (the EGV values in all cells of a raster map of a pre-defined study site). In order to define habitat preferences, ENFA computes two types of uncorrelated factors from the input set of possibly correlated EGVs. Unlike factors produced by traditional factor analyses, such as PCA, these factors are ecologically relevant in that they formally describe some aspect of the species niche relative to the 'global' availability of the modelled set of EGVs. Therefore, these factors are easier to interpret in ecological terms than those produced by PCA (Hirzel *et al.,* 2001, 2002). The factors are known as 'Marginality' (*M*) and 'Specialisation' and retain most of the information conveyed by the EGVs.

The ENFA process is best illustrated by imagining a species *s* which is non-randomly distributed in geographic space according to its preference for a particular range of an environmental descriptor *x,* where the geographic space is described as a set of cells within a raster map of a study site. If an optimum range of values of *x* exists for species *s*, *s* would be expected to be found preferentially in cells of the study site which have values of *x* within this range. This preference is quantified by comparing the distribution of *x* in cells in which *s* is found (species distribution on *x*; x_s) with the distribution of *x* in all cells in the study site (global distribution of *x*; x_g). The distributions x_s and x_g may differ in terms of their means (m_s and m_g respectively) and/or variability (σ_s and σ_g respectively), as shown in Figure 4.1. Where the means of the distributions differ (i.e. $m_s \neq m_g$), the focal species *s* shows some *marginality* with respect to *x*. Where the variances differ (i.e. $\sigma_s < \sigma_g$) the focal species shows some *specialisation* with respect to *x.* In other words, marginality expresses the difference between the global and species means, whilst specialisation expresses the relative narrowness of the occupied range of *x*.

In the formulation of ENFA, Hirzel *et al.* (2002) formally defined marginality (*M*) as the absolute difference between m_s and m_g, divided by 1.96 standard deviations (σ_g) of the global distribution, x_g (Equation 4.1). This represents a univariate version of the extended, multivariate formulation implemented by BioMapper (Equation 4.2) and is supplied here simply to explain the principle. The division by σ_g is included in order to remove any bias introduced by the variance in x_g whilst the coefficient weighting (1.96) of this division ensures that the marginality value computed will generally lie between 0 and ±1, exceeding unity in only 5% of cases where x_g is normal. The binding of marginality between zero and one provides a scale on which to evaluate the computed marginality value. The larger the absolute value of the marginality factor, the further m_s differs from m_g, whilst a value close to zero indicates that the species tends to live in average conditions throughout the SS with reference to all EGVs. The degree of correlation between the marginality factor and each EGV is expressed by a marginality coefficient for each EGV. The greater the absolute value of each EGV coefficient, the greater the contribution this EGV has to the overall marginality, a low value (close to 0) indicates that the species tends to live in average conditions in relation to that EGV, whilst values closer to one indicate a tendency to live in "extreme" habitats. Positive marginality coefficients indicate that the species prefers EGV values that are higher than the global mean ($m_s > m_g$), whilst negative coefficients indicate a preference for values lower than the global mean ($m_s < m_g$). The marginality factor, therefore, expresses both the direction and the amount of difference by which m_s differs from m_g: the preferences shown by the species for each EGV.

$$M = \frac{|mg - ms|}{1.96\sigma} \qquad \text{(Equation 4.1)}$$

$$M = \frac{\sqrt{\sum_{i=1}^{V} m_i^2}}{1.96}$$

where m_i = the coefficient of the marginality of the focal species on ecogeographical variable i, and V = the number of eigenvectors extracted. (Equation 4.2)

$$S = \frac{\sigma g}{\sigma s}$$ (Equation 4.3)

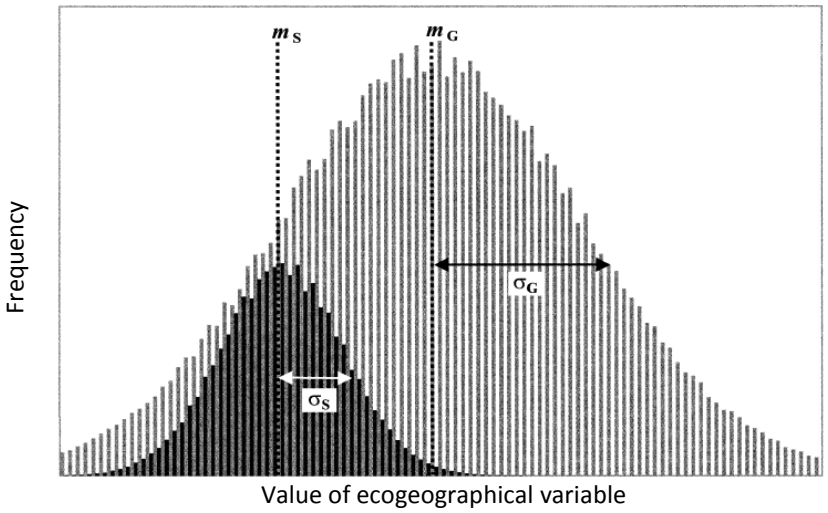


Figure 4.1: A graphical representation of the definition of marginality and specialisation. The distribution of the focal species on any EGV (black bars) may differ from that of the global set of cells with respect to its mean ($m_s \neq m_g$), allowing marginality to be defined, or with respect to its variability ($\sigma_s < \sigma_g$), allowing specialisation to be defined. From Hirzel *et al.,* 2002.

Following the marginality factor, the next factors to be extracted are the eigenvalues known as specialisation factors, which describe how specialised the species is in relation to the range of available EGVs, indicating the range of resource use of each EGV. The marginality factor accounts for a certain proportion of the specialisation (this proportion varies between models) and the residual specialisation is accounted for by the specialisation factors. The *v-1* specialisation factors (where *v* is the number of EGVs) are extracted according to decreasing amounts of explained variance; therefore, the first few specialisation factors to be extracted will typically explain most of the species variability, σ_s. As a large part of the information is contained within the first few specialisation factors, only those that are deemed to be significant by comparison with MacArthur's broken-stick distribution are typically retained in order to compute HS maps; MacArthur's broken stick distribution is the expected distribution when a stick is broken randomly, and the values that are larger than those that would have been obtained by chance are considered significant (Hirzel *et al.,* 2002).

Specialisation coefficients for each EGV range between 0 and ±1, with a high absolute value indicating a narrow niche breadth relative to the range of available conditions. Note that the sign associated with the each specialisation coefficient is simply a product of its computation and is essentially arbitrary: it carries no meaning, unlike the sign for the marginality coefficients. All specialisation coefficients are summarised to give a value for *global specialisation, S*. Equation

4.3 defines *S*, which summarises all of the individual specialisation factors into a single value. Unlike *M*, *S* is not bounded between zero and one but ranges from one to infinity, with any value exceeding unity being indicative of a degree of specialisation; thus, the higher the absolute value of the specialisation coefficients, the more restricted the species is on the corresponding EGV. A randomly chosen subset of cells is expected to have a specialisation of one (i.e. a variance equal to the global variance). As *S* ranges between one and infinity, it is difficult to interpret meaningfully. Instead it is easier to define the breadth of the species niche in terms of the computed tolerance value, *T. T* is simply the inverse of *S* and, as such, ranges between 0 and 1, with low values indicating lower tolerance (high specialisation) and vice versa. Thus, a species with a high *T* value has a particularly wide niche and is generally widespread across the study site.

Equations 4.1 and 4.3 define marginality and specialisation in univariate space. Typically, however, studies into habitat preferences and suitability do not focus on only one EGV, but a range of EGVs which are thought to limit or promote the existence of a focal species in an area. In considering a wider range of EGVs, many studies aim to delineate the ecological requirements of a species in terms of its ecological niche, as defined by Hutchinson (1957). Thus rather than defining preferences as a univariate function, they may be defined, in Hutchinsonian terms, as a hypervolume in the multivariate EGV space (Hutchinson, 1957). When described in this way, the niche may then be defined on any of its axes by an index of marginality or specialisation (i.e. defined by the species mean and range width on these axes, or corresponding EGVs). Some axes may be more interesting and ecologically relevant than others; a factor analysis is therefore used to summarise the axes, transforming the potentially correlated EGVs into the same number of uncorrelated factors (one marginality factor and v-1 specialisation factors) which explain the same amount of variance. A factor analysis is useful as it accounts for linear dependencies between EGVs and may therefore explain some specialisation using these interactions rather than simply analysing the effects of 'raw' EGVs. As outlined above, those factors which are deemed to be least important based on the eigenvalues (in comparison with MacArthur's broken-stick distribution) can then be removed from the analysis without leaving too much information, as would occur in the removal of an entire EGV dataset (Hirzel *et al.,* 2002).

4.1.3 The application of ENFA to grey seals at North Rona

ENFA is being applied here to investigate the habitat preferences of female grey seals at North Rona using a set of EGVs selected based on a basic understanding of their ecological requirements, as reported in previous studies. Previous studies have suggested that fine scale local topography is important in determining the distribution of adult females and the location of pupping sites (Anderson *et al.,* 1975; Anderson and Harwood, 1985; Pomeroy *et al.,* 1994; Twiss and Thomas, 1999; Pomeroy *et al.,* 2000a), and there is certainly scope for female grey seals to

display a degree of site selection when they come ashore to breed. Anderson (1975) suggested that, prior to selecting a pupping site, females come ashore and return to the sea several times. Pomeroy *et al.* (1999) provided support for this suggestion, showing that the mean duration between first sighting of a female and her pupping date was four days. Females show a high degree of pupping site fidelity, returning to within a median distance of 55m of their pupping site in the previous year; they are therefore returning to largely familiar surroundings and have an average of four (but up to 19) days to select a site (Pomeroy *et al.,* 1999). Furthermore, 82% of females were first observed in the vicinity of their subsequent pupping site (Pomeroy *et al.,* 1994). This evidence suggests the possibility of active female choice in pupping site selection, and distinct topographical features on North Rona could be key to female orientation during this process. Therefore, the available habitat on North Rona was quantified at a sub-metre scale and four ecologically relevant EGVs were initially considered for ENFA analysis, as in Chapter 3: elevation, CACC, CPOOL and salinity.

Elevation and CACC were chosen as Twiss *et al.* (2000a; 2001) have demonstrated that sites with intermediate proximity to access points from the sea are preferred as pupping sites and subsequently found an apparent reduction in pup mortality at sites of 'intermediate' elevation and CACC (Twiss *et al.,* 2003). Boyd *et al.* (1962) suggested that the availability of pools of water may be an important determinant of female distribution, and females have long been noted to aggregate around and bathe in such pools, particularly during dry spells (Anderson *et al.,* 1975; Boyd *et al.,* 1962; Pomeroy *et al.,* 1994; Twiss *et al.,* 2000a, 2002, 2007), during which females will incur increased costs in terms of time and energy expenditure in movement between pools and their pup (Redman *et al.,* 2001). Indeed, Pomeroy *et al.* (1994) found that movements towards these pools were the main reason for females moving more than a few metres from their pup between suckling bouts. It is due to this likely increased cost of locomotion over the uneven terrain found on North Rona that 'cost-distance' to pool is being considered for the ENFA, rather than simple Euclidean distance between a female and the nearest pool. Such an approach allows a more accurate depiction of the relative ease or difficulty of moving towards water, based on the slopes and barriers to movement encountered during locomotion (Twiss *et al.,* 2000a). It is thought that pools represent an important resource for thermoregulation, as a means of avoiding thermal stress from overheating (Redman *et al.,* 2001; Twiss *et al.,* 2002). An alternative explanation for preference for proximity to pools is that drinking from these pools aids the maintenance of a positive water balance. It has previously been assumed that grey seals meet their water requirements whilst hauled out through the metabolism of fat reserves (Schweigert, 1993), with no clinical evidence having been found for dehydration during this time, at least in other pinnipeds (Irving, 1935; Kooyman and Drabek, 1968; Ortiz *et al.,* 1978). However, Reilly *et al.* (1996) found that lactating females on North Rona incurred a negative water balance; females

at North Rona have also been observed drinking from pools of water (Reilly *et al.,* 1996; Redman *et al.,* 2001; PPP and SDT, *pers. comm.*). The reason for the differences in conclusions as to water requirements may be, as suggested by Redman *et al.* (2001), that the average temperature on North Rona is approximately 7°C higher than Nova Scotia, the colony at which previous water balance research was performed (Redman *et al.,* 2001); this may be enough to induce additional water requirements on North Rona. Therefore, pool salinity is also being considered in the ENFA, because, if pools are necessary for drinking as well as cooling, females may exhibit a preference for pools with fresher over more brackish water.

In order to determine the site preferences of female grey seals, two approaches to the ENFA were taken. First, the ENFA was performed with female presences as input, in order to determine female habitat preferences. The second approach was to use pup locations as input, as an indication of pupping site selection. In this approach, only the positions of younger (Stage I and II; neonate) pups were considered, as they are typically less mobile than older pups, and their location is therefore more likely to represent the location of the actual pupping site. The use of these two approaches is also useful in that it may outline differences in the preferences that females show in their pupping site selection and in their subsequent use of the available habitat, should this differ from the conditions at the pupping site. This seems especially likely given the great distances that females sometimes move from their pups, for example to reach pools of water (Redman *et al.,* 2001). Therefore, conditions at female locations will be used to assess what shall be termed 'habitat preferences', whilst conditions at neonate locations will be used to assess what shall be termed 'pupping site preferences'. In the present study, the most important products of ENFA computation are the marginality and specialisation (or tolerance) coefficients. These essentially define the preference of the seals for each EGV in turn, describing not only the importance of each EGV in explaining the current seal distribution but also describing their preferences for EGV values that are either higher or lower than the global mean.

Although much research (outlined above and in Chapter 2) has assessed the influence of topography on female distribution, the work presented in this thesis is novel in its use of up-to-date topographic data (pool distribution, salinity) and in that it directly quantifies preferences through the use of SDMs, determining and ordering the importance of particular EGVs. By contrast, earlier studies of habitat choice have been based on qualitative habitat descriptions or simplistic models utilising hierarchical selection procedures within the GIS, rather than using factor analyses of all variables simultaneously. Following an outline of the methods used throughout this chapter (Section 4.2), the results are presented in Section 4.3 and are discussed largely in Section 4.4, though may be discussed briefly throughout Section 4.3 where appropriate, as this discussion informs some of the subsequent results.

4.2 Methods

This section describes the method for outlining the environmental preferences of female grey seals and modelling HS. The ENFA input are described and explained (Section 4.2.1) before the ENFA protocol is outlined and the ENFA output described (Section 4.2.2). The processes of HS mapping (Section 4.2.3) and discriminant analysis (Section 4.2.4) are then described.

4.2.1 ENFA input

4.2.1.1 Presence data

The female and neonate presence data was collected by PPP as described in Section 2.4 (2.4.1; 2.4.2). This gave a total of 4366 presences (3013 female and 1353 neonate locations) spread unequally throughout the 15 focal dates, as indicated in Table 3.6. The number of presences used in exploratory analyses (Chapter 3) considering every day of all five breeding seasons totalled 50372 (31399 female and 18973 neonate locations). Only data from individual focal dates were used in ENFA analyses, rather than pooling data from multiple days. To create a Boolean grid map of seal presences at the same resolution as the EGV maps, as required for ENFA analysis, female and neonate GIS coverages were converted to grids (an alternative Arc format) of 0.2m × 0.2m resolution. These grids were aggregated to a coarser 1m × 1m grid cell size, with each cell conveying the presence or absence of seals in that area (e.g. Figure 3.16, Section 3.3.3).

4.2.1.2 Ecogeographical variable data

The SS, as defined in Section 2.3, was characterised using the four EGVs Elevation, CACC, CPOOL and salinity at a 1m × 1m grid cell resolution. The collection and manipulation of the EGV data is described in Section 2.4. CACC and elevation were constant over the breeding season and between years, as these describe permanent features of the island of North Rona itself, and so were computed only once. Conversely, CPOOL and salinity were variable within and between seasons, so a new grid was created for each survey date, as described previously (Section 2.4). See Figures 3.1-3.4 (Section 3.3.1) for sample representations of EGV distributions across the SS.

4.2.1.3 Importing data to BioMapper

All species and EGV maps were converted to ASCII files and imported to IDRISI32 in order to convert them to raster maps suitable for use in BioMapper, in which all maps were verified to ensure identical extents, removing discrepant cells (Section 2.4.5). All resulting maps were composed of 82223 × $1m^2$ cells (Figure 2.6). Initial exploratory analyses found CACC and elevation to be highly correlated at a global scale (i.e. over the SS) and so the redundant variable ELEV was removed from all subsequent analyses. Correlation was assessed via the construction of a UPGMA (Unweighted Pair Group Method with Arithmetic Mean) correlation tree (Sokal and Michener,

1958), the default method of assessing correlation through BioMapper. This returned a correlation coefficient of 0.896. ELEV was chosen for removal over CACC as the latter incorporates more information; whilst ELEV includes only the elevation profile of North Rona, CACC includes ecologically relevant information such as impassable barriers and a 'target' (e.g. access points) for movement (Section 2.4). This means that, whilst two points may have the same elevation value, one may have a dramatically lower CACC value due to its relative proximity to access, which is demonstrably important for grey seal site choice (Twiss *et al.,* 2000a; 2001). The ability to remove correlated EGVs in this way is a major advantage that ENFA, as applied in BioMapper, has over stepwise regression analyses such as GLMs, GAMs and logistic regression: with these techniques, variables are not included in the final model if they do not explain a significant amount of the total variance. In a case such as this, where two variables (CACC and elevation) exhibit some form of correlation, one will be arbitrarily rejected by the model; however with ENFA if two variables are correlated they both appear in the final model with a similar coefficient and the decision of which (if either) to reject is left to the ecologist rather than an ecologically blind algorithm.

Theoretically, multi-normality of input variables is required for factor extraction based on eigensystem computation (Legendre and Legendre, 1998). Tests for normality (Kolmogorov-Smirnov tests) of each EGV were therefore performed within BioMapper. All EGVs had positively skewed, non-normal distributions. In past literature, following recommendations associated with ENFA and BioMapper (Hirzel *et al.,* 2002; Hirzel, 2008), there has been a tendency for all non-normal EGVs to be transformed towards normality using the Box-Cox transformation algorithm (Box and Cox, 1964; Sokal and Rohlf, 1981). This method estimates lambda, the Box-Cox transformation coefficient, which transforms the data such that it best approximates a normal homoscedastic distribution. Lambda is the value to which the data is power transformed and can take on an almost infinite number of values (e.g. $\lambda = 0.50$: square root transformation; $\lambda = 0.25$: 4^{th} root transformation; $\lambda = -1.00$: reciprocal (inverse) transformation).

However, as a large part of this investigation is to analyse change in preferences over time, the Box-Cox transformation would only have been appropriate for CACC, which is constant over time. Salinity and CPOOL are variable over time and the method of assigning lambda values by the Box-Cox algorithm resulted in the use of a different lambda value for each different salinity and CPOOL map. This means that the maps of either salinity or CPOOL from different time points were transformed differently. Transformed maps and ENFA results based on these transformed maps would no longer be comparable between time points. Furthermore, the CACC and CPOOL data both contain 'real' zeros; this makes transformation difficult as it is not possible to power transform zeros. In order to transform such data, a constant would need to be added to all data to remove zeros by 'shifting' the data, as was performed for the statistical analyses in Chapter 3. Such an approach was deemed unsuitable here due to the applications of the data. ENFA analyses

EGVs and the interactions between them, so applying a shift would alter the interactions depending on the constant added. Furthermore, the application of transformations, particularly reciprocal transformations, would cause difficulty in interpretation of the ENFA output in real ecological terms. All EGVs were therefore left untransformed; this was deemed reasonable as previous studies have found that methods utilising factor extraction, including ENFA, are typically robust to deviations from normality (Glass and Hopkins, 1984; Hirzel *et al.,* 2002; Titeux *et al.,* 2007) and that the transformation stage "can as well be ignored" (Hirzel, 2008).

4.2.2 ENFA protocol

ENFA was performed within the software BioMapper 4.0 (Hirzel *et al.,* 2007). BioMapper implements ENFA using raster maps of species presence points and EGV layers (Sections 2.4 and 4.2.1). Boolean raster maps of female and neonate presence were input to BioMapper along with untransformed raster maps of CACC, CPOOL and salinity for all 15 focal dates; all raster maps had a grid cell resolution of $1m^2$. BioMapper was used to compute the ENFA and HS maps separately for both the female and neonate presence datasets on all individual focal days using all three variables (separately for each focal day). For each iteration of the ENFA, one marginality factor and two specialisation factors were computed, each of which represents a linear combination of the EGVs. The technical aspects of ENFA computation have been explained in Section 4.1.2 and the ENFA and HS mapping processes are summarised in Figure 4.2, whilst the HS mapping procedure is outlined in Section 4.2.3. The overall niches of females and neonates were evaluated using the global marginality, specialisation and tolerance values produced by ENFA, which summarise the information contained in the ENFA factors into values which describe the species' habitat preferences and tolerance of environmental change. The overall marginality and tolerance values of both the females and neonates during each year were compared across the early, mid and late stages of the breeding season to ascertain whether these values show any consistent trend in change across the season. The comparison was carried out using randomisation tests analogous to a between-subjects one-way ANOVA (Todman and Dugard, 2001); this approach was used due to the small sample sizes in each group. The randomisation tests were carried out using a Microsoft Excel macro provided by Todman and Dugard (2001); the macro computes the test statistic (residual sum of squares; RSS) for the actual data and then for 1000 randomly chosen arrangements of the data that conform to the numbers of observations (marginality or tolerance values) per condition (Stage of breeding season) derived from the data. The proportion of RSS values that are smaller than the actual RSS value is the required probability for statistical significance (Todman and Dugard, 2001). Only the early, mid and late stages were considered in this analysis as these are the stages common to most seasons.

4.2.3 Habitat suitability mapping

HS maps were created for females and neonates on each focal date using the Distance Geometric Mean algorithm (Hirzel and Arlettaz, 2003; Hirzel *et al.,* 2004), based on the ENFA-derived eigenvalues. Of the five algorithms available in BioMapper, this seemed the most appropriate for the data presented here as, unlike the alternatives, it makes no assumptions regarding the species distribution and assigns higher HS values to areas in which seals are more densely aggregated (Hirzel and Arlettaz, 2003). This seems a reasonable approach, as Twiss *et al.* (2001) suggested that females aggregate around habitat features with variation in density according to the HS of that location. Furthermore, it was assumed that including the density of observations in the modelling procedure would not introduce any bias stemming from the differences in detectability of the seals across the SS or any observational bias stemming from the sampling regime, which ensured that all seals were mapped, whilst observer location ensured good detectability of all seals within the SS. The distance harmonic mean algorithm also makes no assumption on the species distribution, but was deemed unsuitable as it gives a very high weight to each single observation and is therefore more appropriate when sample sizes are very small.

During HS map creation, the decision of which ENFA-computed factors to retain for the final model was based on inspection of eigenvalues alongside MacArthur's broken stick method (MacArthur, 1960; Hirzel *et al.,* 2002). For all ENFA iterations three factors were computed and all were kept for HS computation in every case. The process of HS map computation performed in BioMapper results in each cell of a raster map being assigned HS values based on the combination of factors (and thus EGVs) in that cell, as depicted in Figure 4.2. These HS values are normalised such that the HS index ranges from 0 to 100% (Hirzel *et al.,* 2002). The HS models were evaluated using Jack-knife cross-validation (Fielding and Bell, 1997; Boyce *et al.,* 2002). For each map, the species locations were partitioned into k mutually exclusive but identically sized sets. This partitioning was performed with the random seed value set to one, and the 'randomness field' set to 100%; this ensures that points are partitioned 50% by random and 50% by geographical position, making the cross-validation more robust to potential spatial auto-correlation, e.g. resulting from conspecific attraction. The validation procedure was carried out such that k-1 partitions were used to compute a HS map and the left-out (k^{th}) partition used to validate this map on independent data. This process was repeated k times, each time using a different partition for validation, resulting in k largely different HS maps. The number of partitions used was chosen based on Huberty's Rule (Fielding and Bell, 1997); a rule of thumb for determining the ratio of calibration and validation points. This rule suggests a ratio of $1/(1+\sqrt{(V-1)})$, where V is the number of EGVs (Fielding and Bell, 1997). The number of partitions was, therefore, set to two, resulting in a validation method similar to that used in many niche modelling studies, which use half of the presence data for calibration and half for validation of models (Fielding and Bell, 1997).

The HS maps were then validated based on their fluctuations relative to one another, using the Continuous Boyce Index (CBI; Boyce *et al.,* 2002; Hirzel *et al.,* 2006) with a window size of 20. This validation method is insensitive to species prevalence (Hirzel *et al.,* 2006), which is important given the varied sample sizes between focal dates. The CBI does not assess the predictive ability of each model *per se*, but instead assesses the ability of each model to consistently predict levels of suitability (Hirzel *et al.,* 2006).CBI evaluates the relationship between the predicted (P_i) and expected (E_i) number of validation (species presence) points found at all HS values within a moving window of a fixed width (W). Computation of the CBI starts with a first window covering the HS range 0-W, from which the ratio (P_i/E_i) of predicted (P_i) to expected (E_i) species points within this HS range is plotted, before the window is shifted and the P_i/E_i ratio is plotted again. This is repeated until the entire HS range has been covered and a smooth predicted to expected curve is plotted. The CBI uses Spearman's rank correlation to assess the monotonic increase of the P_i/E_i ratio when plotted against HS, producing a CBI value which may range from zero to one, with larger values indicating better performance (better consistency between models). The index is explained in more detail in Hirzel *et al.* (2006). Also important in assessing HS models quality is a visual assessment of the validation (P_i/E_i ratio) curves (Hirzel *et al.,* 2006), which indicate how well the models discriminate between different quality habitats. Hirzel (2008) summarised the information conveyed by the shape of these curves as follows:

- Linear: Best case; model discriminates well between all HS values and site suitability is essentially proportional to the probability of its use (Manly *et al.,* 2002).
- Exponential: Good; a low plateau at the start of the curve indicates poor discrimination between low-quality sites, but discriminates high-quality sites reliably.
- Sigmoid: OK; discriminates low-quality sites poorly and mid-quality sites well. High quality sites are distinct from mid-quality sites.
- Saw-toothed: Unreliable, with lots of variance in the saw-toothed region of the curve.
- Flat line: Very poor; model does not perform much better than a random model.

Any departure from a straight line with positive slope essentially equates to a decrease in model resolution, and any region of the P_i/E_i curve with a flat or negative slope may be pooled to represent one class of HS values, rather than a continuous measure of suitability. This decrease in resolution is also reflected in the CBI score. The variance among the P_i/E_i curves demonstrates how robust the model is in terms of assessing suitability along the entire range of HS values. As the variance tends to vary along the P_i/E_i curves, a visual assessment of this variance is helpful in determining which parts of the model are most accurate. It is also possible to obtain information regarding the deviation of the model from random from the P_i/E_i curves; however, because this is highly dependent on the population niche breadth, this will be considered only when comparing female models with other female models (i.e. not between females and neonates).

HS maps produced by BioMapper for this research were not intended for use as predictive maps, but were used to assess (visually and statistically) how the distribution of high and low-quality habitat changes within and between seasons (Section 4.3.4).

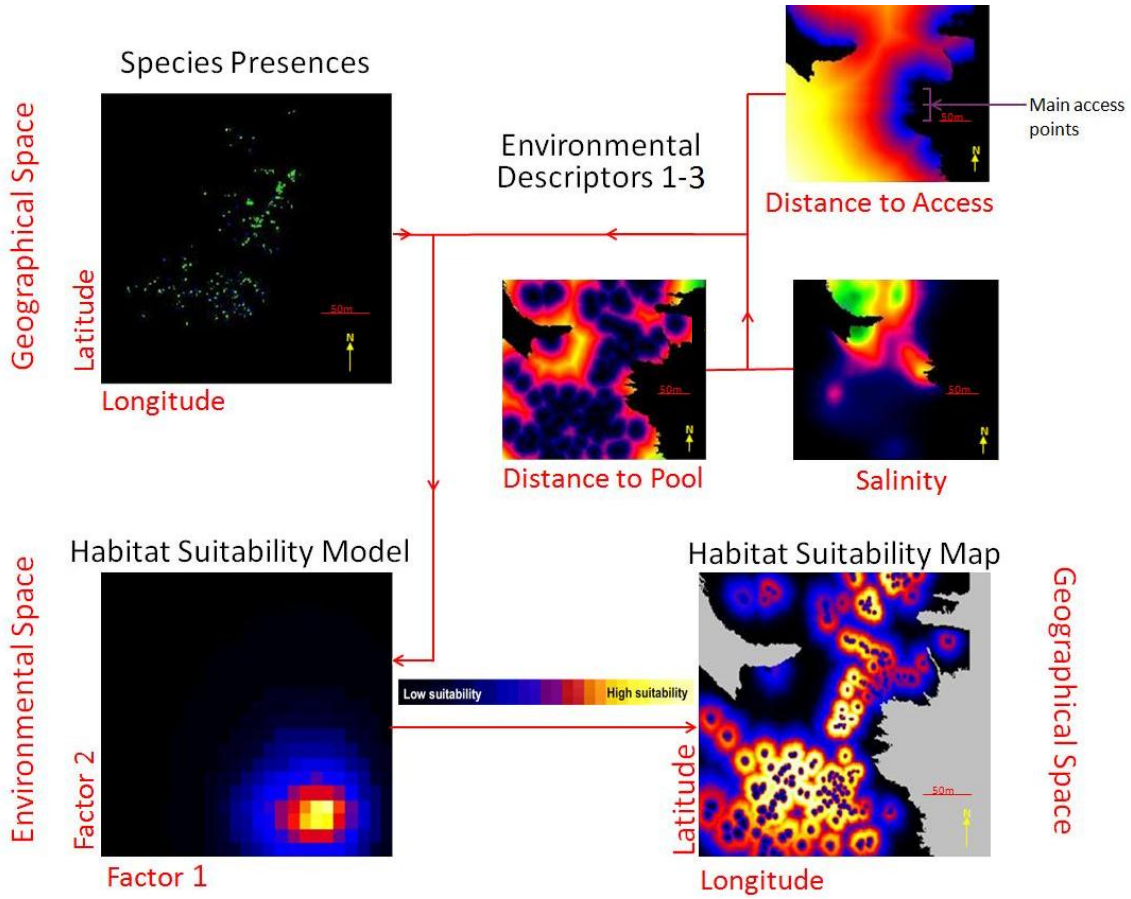


Figure 4.2: Graphical summary of the ENFA process, using appropriate EGVs and female grey seal distribution from the North Rona SS on October 24th 2009. Areas of land on EGV maps are coloured such that brighter colours represent high values, whilst red through blue and black represents low values.

4.2.4 Discriminating between adult female and neonate niches

Discriminant analysis (DA; Legendre and Legendre, 1998) was used to compare the niches of females and neonates in a pairwise fashion on focal dates to determine which EGVs were responsible for any niche divergence between these age classes. DA is implemented within BioMapper and directly compares the EGV values of two 'species' (in this case age class) distributions; it differs in this respect from ENFA, which compares the distribution of one species to the 'global' distribution of EGVs. DA computes a factor which both maximises the separation between the distributions of the two age classes and minimises the variation within each age class. As with ENFA-computed factors, the coefficients of this factor can easily be interpreted in terms of the input EGVs to determine how resource use of the two age classes differs. DA provides N_s - 1 eigenvalues (where N_s is the number of input seal location maps). These eigenvalues indicate the ratio of between-age class to within-age class variance; the higher these eigenvalues, the greater the amount of niche (resource use) separation that exists between the N age classes, whilst eigenvalues less than 1 indicate very similar niches. DA also produces N_s-1

discriminant factors, each of which is represented by a coefficient relating to each EGV. These coefficients indicate how well the corresponding EGV separates the age class niches (i.e. a high coefficient value for CPOOL would indicate that the age classes differ in their preferences for proximity to pools). A graph is produced similar to Figure 4.3 which shows the distribution of each age class on the discriminant factor. Where age classes are highly discriminated, one will be mostly distributed in the positive values and one in the negative values (the 'positive age class' and 'negative age class' respectively, Figure 4.3A). Where coefficients of the discriminant factor are negative values, high values of the corresponding EGV 'favour' the 'negative' age class. Conversely, positive coefficients indicate that high values of the corresponding EGV 'favour' the 'positive' age class (i.e. a coefficient of +0.674 for CPOOL would indicate that the 'positive' age class is typically found further from pools than the 'negative' age class).

BioMapper incorporates some of the commonly used measures of niche breadth and overlap (Hirzel *et al.,* 2007). Comparisons of competing breadth and overlap measures have generally concluded that those most commonly used produce similar results, and that none may be judged to be better than the others (Krebs, 1999; Zabala *et al.,* 2009). Here, niche overlap was analysed using Pianka's Overlap Index (Hurlbert, 1978) as it is in widespread use and is easily interpretable as its values range from 0 to 1. Niche breadth was not analysed in this way as this function is performed by comparison of species specialisation coefficients produced by ENFA.

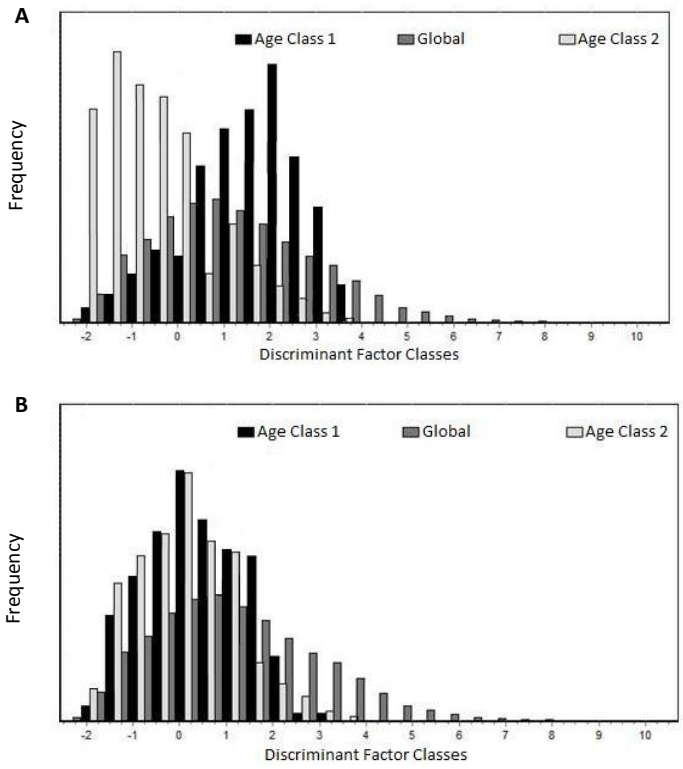


Figure 4.3: The distributions of discriminant factor values 'globally' and for two hypothetical age classes based on fictitious EGV values. **A:** The positive and negative age classes can be easily distinguished based on their distribution on the discriminant factor, and discriminant analysis can be performed; **B:** The positive and negative age classes cannot be easily distinguished based on their distribution, making the output of the discriminant analysis uninterpretable.

4.3 Results

The ENFA was performed on data from all 15 focal dates for the females (dates shown in Table 2.1; Chapter 2); however, the small sample size for neonate presences at the beginning of the 2010 season (n = 19) produced a nearly singular 'species' correlation matrix and so the ENFA could not be performed. Therefore, this date was excluded from the neonate analyses.

4.3.1 Ecological niche of adult female grey seals

In summary, ENFA showed that female grey seals tend to occupy areas in which conditions depart only moderately from the average conditions available over the SS (are slightly marginal; Section 4.3.1.1) and that they tend to occupy a restricted range of EGV values relative to that which is available (are relatively specialised; Section 4.3.1.2). This specialisation is clearer early in each breeding season when compared to later in the season, when females appear to occupy a wider range of EGV values. Integrating these results with those from Chapter 3 indicates that the restricted range of EGV values occupied by females is a consequence of avoidance of extreme values, with females typically occupying intermediate values for all EGVs. CPOOL contributes the most to female grey seal marginality, meaning that this is the EGV on which the mean of the female distribution differs most from the global availability, whilst the EGV contributing most to the specialisation is more variable between focal days (Section 4.3.1.3). The changes in marginality, specialisation and tolerance coefficients over each breeding season suggest a change in preferences, or may be indicative of restricted choice later in the season (Section 4.3.1.3). Furthermore, there are a small number of coefficients (especially those for 2009) which do not match the trends; this warrants further exploration in Section 4.3.1.4.

4.3.1.1 Marginality of female distribution

The marginality coefficients returned for the females demonstrates a tendency for female seals to inhabit areas with conditions which depart only moderately from the average for the SS. Table 4.1 shows that all global marginality values are greater than zero, though with none exceeding 0.5. As noted above, high marginality values (close to 1) indicate that seals are typically found in extreme conditions relative to the SS, whereas low values (close to 0) indicate a tendency to be found in average conditions. Though the marginality values are relatively low, their variability across each season may be informative. The global marginality value for females on a given day is variable both across and within seasons, with a general decreasing trend across the season (Table 4.1 and Figure 4.4). This is evident in all years analysed, however, there does was no consistency in female marginality within breeding season stages across the five years (Randomisation Test; RSS = 0.111, p = 0.348). However, this does not imply that within season changes are non-significant, only that marginality cannot be predicted by breeding season stage.

This may be due to changes in EGVs between seasons, but may also be due to the fairly loose definition of breeding season 'stage', each of which encompasses a range of days.

The general decrease in marginality across each season is due to females being found in increasingly 'average' sites as the season progresses. This may be interpreted in one of three ways: (i) as the season progresses, more females 'choose' pupping sites with EGV values closer to the average available across the SS; (ii) as the season progresses, more females are 'forced' into more average areas by presence of females at 'preferred' sites; (iii) as the season progresses, fewer sites with more 'extreme' EGV values are available, with each site having EGV values closer to the global average; as a result the range of sites that females can choose from is less variable. These alternative interpretations are potentially co-incidental, though the results of Chapter 3 indicate which is the most likely; in Figures 3.3 and 3.4 it is clear that for those EGVs that vary across the season (i.e. salinity and CPOOL) there was generally greater variability, with larger variances and greater spread of values later in each season. Furthermore, the minimum of each EGV did not increase between stages within breeding seasons, suggesting that a change in availability of preferred sites has not necessitated female movement into less preferred areas. This suggests that the decrease in marginality over each season is due to female choice or forced movement, rather than declining availability of preferred sites as a result of EGV changes.

4.3.1.2 Specialisation of female distribution

The global specialisation values suggest a tendency for female grey seals to occupy a restricted range of EGV values relative to that which is available on average over the SS. As with marginality, the global specialisation values are variable across and between breeding seasons. However, as Table 4.1 shows, there is a general trend for a decrease in global specialisation over the course of a breeding season. This means that, in general, females occupy sites covering a wider range of EGV values later in each season. This is contrary to what might be expected; as the SS gets wetter over the season, one might expect lower variation in CPOOL as all points are closer to pools, though this does not appear to be the case. However, there are a number of discrepancies (explored in Section 4.3.1.4), such as the increase in specialisation between the early and middle stages of the 1998 breeding season. Additionally specialisation increases between mid- and late- 2008. The only other discrepancy is a large increase in global specialisation between late and end 2009. Specialisation, which ranges between one and infinity, is difficult to interpret and so more attention will be given to the tolerance value ($T = 1/S$).

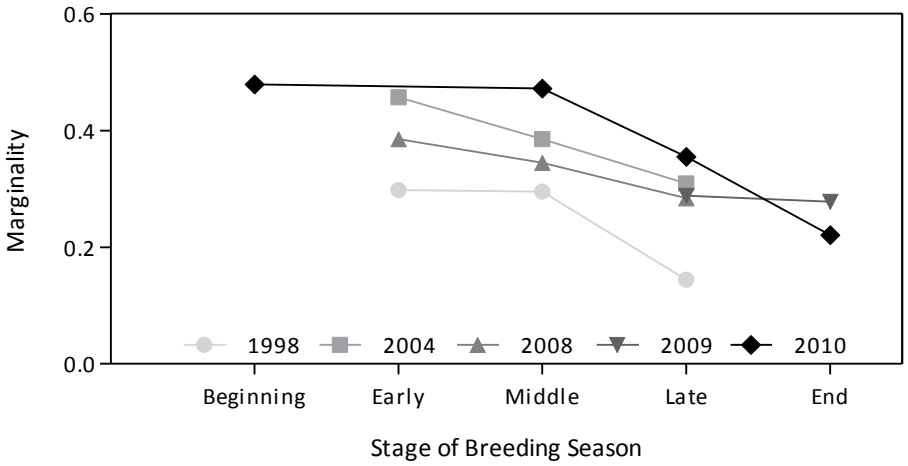
As global tolerance is the inverse of global specialisation, it is inevitable that the same trend should be seen in both. There is a general trend for the global tolerance to increase over the season, again with some notable exceptions, though there is no consistency in female tolerance within breeding season stages (Randomisation Test, RSS = 0.214, $p = 0.122$). This does not imply

that within season changes are non-significant, only that the tolerance cannot be predicted by breeding season stage. As with marginality, this may be attributed to either inter-seasonal global EGV change or the fairly loose definition of breeding season 'stage'. As expected, given the specialisation values, the tolerance coefficient for early 1998 is high relative to the middle of the season, whilst that for the end of the 2009 season is relatively low. Furthermore, though there is a general increase in tolerance over the 2008 season, there appears to be a 'spike' in tolerance in the middle of the season. Tolerance ranges between 0 and 1, with low values indicating a degree of specialisation in terms of the ecological niche, with females tending to occupy a narrow range of conditions relative to the rest of the SS. Conversely, high values indicate that the species tends to occupy a wide range of conditions relative to that available over the SS. Female grey seals appear relatively specialised in terms of habitat choice at the beginning of each season, as demonstrated by the low tolerance values at these times. In other words, female grey seals occupy a relatively narrow range of conditions relative to that which is available, though the range of EGV values occupied is generally wider as the season progresses. This is especially clear for the beginning of the 2010 season, which may be particularly informative as it represents the earliest day of the breeding season analysed in this study. Given the high specialisation (low tolerance) exhibited at the beginning of the 2010 season it is difficult to say how large the fluctuations in specialisation and tolerance are during the early to end stages of each season are. As discussed in Section 6.2.4 more data would be required from the beginning of each season to shed light on this, though the availability of aerial photographs for extraction of pool data limits this possibility.

Table 4.1: Global marginality, specialisation and tolerance values for females on all 15 focal dates.

ENFA Output Type	Stage of Breeding Season	Year					
		1998	2004	2008	2009	2010	Average
Marginality	Beginning					0.479	0.479
	Early	0.298	0.457	0.385			0.380
	Middle	0.295	0.385	0.345		0.472	0.374
	Late	0.144	0.309	0.284	0.288	0.355	0.276
	End				0.278	0.221	0.250
Specialisation	Beginning					5.951	5.951
	Early	1.335	2.050	2.010			1.798
	Middle	1.496	1.826	1.785		1.856	1.741
	Late	1.191	1.778	1.946	1.303	1.557	1.555
	End				2.357	1.434	1.896
Tolerance	Beginning					0.168	0.168
	Early	0.749	0.488	0.497			0.578
	Middle	0.669	0.548	0.560		0.539	0.579
	Late	0.840	0.562	0.514	0.767	0.642	0.665
	End				0.424	0.697	0.561

A



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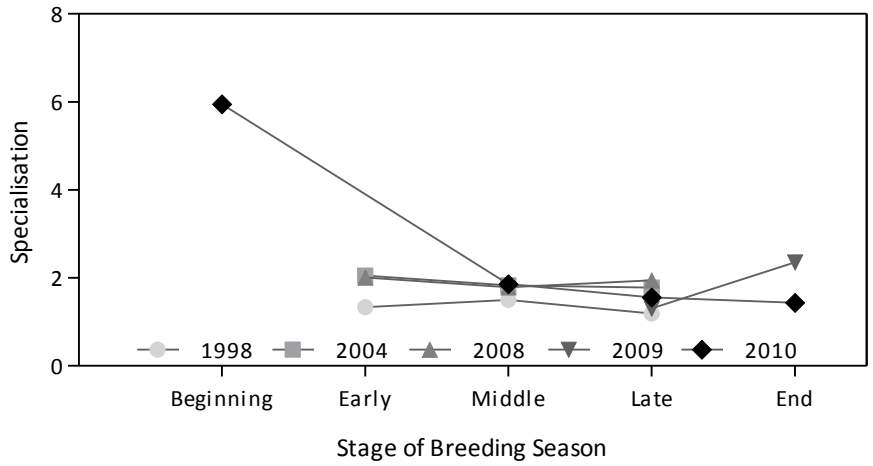

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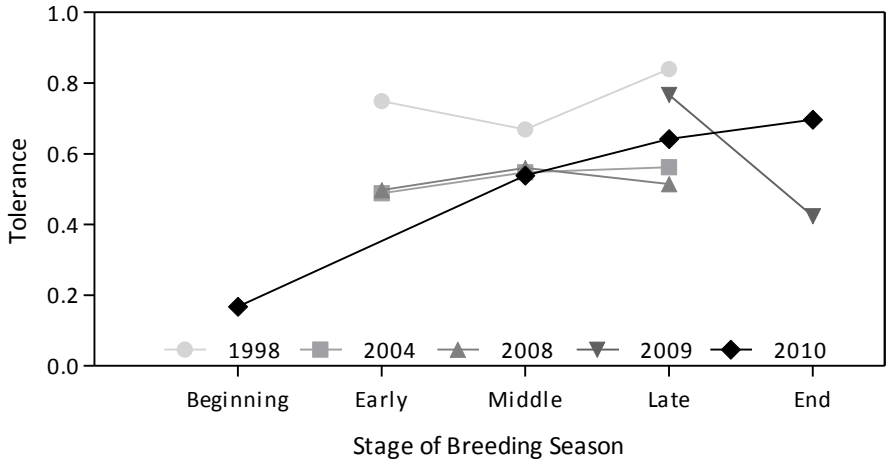


Figure 4.4: Change in female marginality, specialisation and tolerance throughout all five breeding seasons. **A:** Marginality; **B:** Specialisation; **C:** Tolerance (=1/Specialisation).

4.3.1.3 Determination of EGV preferences

All EGVs included in the ENFA were found to be associated with grey seal habitat selection, though each EGV contributes differently to the marginality and specialisation between focal days. Table 4.2 shows the coefficients of each EGV on the three factors for each model run. This table also includes information from the scores table produced by BioMapper, which replaces negligible EGV coefficients with '0'. The three factors computed accounted for 100% of the total sum of eigenvalues (that is, 100% of the marginality and 100% of the specialisation) in every case. The first factor (marginality factor) accounts for the total marginality and a certain percentage of the specialisation (indicated in Tables 4.2 and 4.3 in the '% S' rows), which is variable between focal days, ranging between 31% and 78% of total specialisation. The remainder of the specialisation is accounted for by the subsequent specialisation factors (S1 and S2).

The marginality coefficients for each EGV (Table 4.2), which are generally negative or equivalent to zero, indicate that where a 'preference' exists, female grey seals 'prefer' sites close to pools of low salinity that are near to access points. CPOOL is the EGV that contributes most to the marginality of female grey seals in each model run (Table 4.3); in other words CPOOL is the EGV on which the distribution of females differs most from the distribution of available sites over the SS. All CPOOL marginality coefficients are negative and very large (Table 4.2), indicating that seals 'prefer' sites with much lower 'cost-distance' to pool than is available on average over the SS. However, it is important to note that the seals tend not to occupy sites with very low CPOOL but instead opt for sites at intermediate CPOOL, as shown in Chapter 3. The EGV with the second largest marginality coefficient is CACC in the majority of cases, though this is variable between focal days. In almost all cases, the salinity and CACC marginality coefficients are negative or equivalent to zero (Table 4.2). This suggests female preference for sites with lower than average salinity values closer to access points. The computed coefficients indicate that salinity contributes to female marginality in 13 of the 15 model runs. This can be seen in Table 4.2, which also demonstrates (denoted by '0') that salinity was not deemed important for two model runs (mid-2004 and mid-2010). Of these 13, only two coefficients (late and end 2009) suggested that females 'prefer' sites with higher than average salinity; this will be elaborated upon below and in Section 4.4. However, the remainder of the coefficients (11 out of 15) suggest that females strongly prefer sites with lower than average salinity.

The EGV specialisation coefficients indicate how restricted the range of the seals is on the corresponding EGV. The specialisation factors each account for a large proportion of the observed specialisation (mean = 26.5%, minimum = 7%), and a degree of specialisation on both salinity and CACC is seen on at least one of the specialisation factors on each focal day (Table 4.2). This indicates that throughout the season females tend to occupy sites within a relatively restricted

range of salinity and CACC. CPOOL consistently appears to have the lowest absolute specialisation coefficients. However, this is misleading because a large proportion of the specialisation is accounted for by the marginality factor (Section 4.1.2). CPOOL not only contributes the most to marginality in all cases but also contributes the most to specialisation in over half of the cases (Table 4.3). This demonstrates that female grey seals typically occupy sites with a restricted range of CPOOL values that differ from the average over the site. Tables 4.2 and 4.3 demonstrate that CACC and salinity both contribute considerable amounts to female specialisation, indicating a tendency to occupy sites within a restricted range of these EGVs. This is supported by the evidence presented in Chapter 3, which indicate a tendency for females to occupy sites of intermediate CACC and salinity, avoiding the extreme high and low values for these EGVs.

Interestingly, those dates with *marginality* coefficients indicating a preference for high CACC and salinity (Table 4.2) are associated with *specialisation* coefficients for that EGV which are considerably lower than the specialisation coefficients for other EGVs on that date (Table 4.3). This suggests that, for example, where the marginality values indicate a preference for sites of high salinity, the adult females are actually distributed across a wide range of salinity (e.g. in 2009). This association between marginality and specialisation allows us to infer that higher values of CACC and salinity are generally occupied when the population as a whole is spread over a wider range of sites or, in other words, that when the female niche is narrower, preferences for low CACC and salinity are clearer. It is also possible that the preference for sites of high salinity is simply an artefact of the salinity interpolation technique; this is explored further in Section 4.4.

4.3.1.4 Intra-seasonal change in EGV preferences

The magnitude of the marginality coefficients indicates importance of the corresponding EGV to overall female marginality, and it is interesting to evaluate their change within each breeding season (Figure 4.5). Females appear to 'prefer' sites progressively further inland as each season progresses, as indicated by the change in CACC marginality coefficients, which tend to become 'less negative', demonstrating a shift towards higher values of CACC closer to the SS average (Table 4.2 and Figure 4.5A). For example, the CACC coefficient changes from -0.402 at the beginning of the 2010 season to -0.131 at the end of the season. Female grey seals prefer sites close to pools throughout all breeding seasons, though as each season progresses females tend to be found in sites with more average CPOOL values, exhibiting less of a preference relative to the global availability of pools (Table 4.2 and Figure 4.5B). A similar trend to the CACC marginality coefficients is seen in the salinity coefficients (Table 4.2 and Figure 4.5C), indicating that females tend to be found in areas of higher salinity and CACC later in the season than earlier in the season, relative to the prevailing conditions. In general, there is a decrease in the importance of salinity in determining female distribution between the earlier and later stages of each season, as indicated

by the decrease in absolute coefficient size between the first and last stage of each season (except for 2009). For example, the value of the salinity coefficient changes from -0.357 to -0.191 between the beginning and end of the 2010 season. However, although there is an overall decrease in importance, salinity coefficients increase between the penultimate and latest stage of the 2004, 2008 and 2010 seasons, indicating that females occupy sites with salinity values closer to the global average in the middle of these seasons. This may be a result of the greater numbers of females ashore in the middle of each season, relative to early and late in the season, forcing the use of a wider range of (less preferred) sites. This is not evident in 1998, possibly because the number of females ashore does not decline at the end of 1998 as it does in other seasons.

The marginality coefficients therefore show that female grey seals are essentially linked to sites close to pools (closer than the average location) which are typically of lower salinity than is available on average over the SS. There is an overall preference for these sites to be located close to access points earlier in the breeding season, but with low CACC and salinity becoming less important as the season progresses as females move further inland and towards sites of higher salinity. The range of specialisation coefficients (Tables 4.2 and 4.3) indicate that females are relatively tolerant of a fairly wide range of conditions, but occupy a restricted range of values on each EGV that typically widens as the season progresses and sites with a greater range of EGV values become occupied.

Table 4.2: Coefficients of EGVs on each ENFA factor for female grey seals on each focal day. The marginality factors explain 100% of the marginality and a certain amount of specialisation; '%S' indicates the amount of specialisation (S) accounted for by each factor; CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest coefficient value on each factor.

Stage of Breeding Season:		Beginning			Early			Middle			Late			End		
Year	**EGV**	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]
1998	**CACC**[3]				-0.604	-0.519	**0.636**	-0.344	0.555	**0.762**	-0.084	**-0.993**	0.056			
	CPOOL[3]				**-0.740**	0.083	-0.671	**-0.905**	0	-0.424	**-0.994**	0.090	-0.081			
	SAL				-0.296	**0.851**	0.380	-0.248	**-0.831**	0.490	-0.076	-0.076	**0.995**			
	(% S)				35	38	26	43	33	24	38	36	26			
2004	**CACC**[3]				-0.280	**0.941**	-0.365	-0.051	**0.996**	-0.197	-0.228	0.541	**0.799**			
	CPOOL[3]				**-0.920**	-0.206	0.368	**-0.999**	-0.052	0	**-0.961**	0	-0.277			
	SAL				-0.276	-0.267	**-0.855**	0	-0.076	**-0.980**	-0.158	**-0.841**	0.534			
	(% S)				64	25	11	67	22	11	48	28	24			
2008	**CACC**[3]				-0.525	0.664	0.427	-0.156	0.670	**-0.731**	-0.057	0	**0.993**			
	CPOOL[3]				**-0.698**	0	**-0.711**	**-0.980**	0	0.198	**-0.950**	0.308	-0.086			
	SAL				-0.488	**-0.747**	0.558	-0.123	**-0.742**	-0.653	-0.308	**-0.951**	0.083			
	(% S)				31	47	21	35	45	20	48	34	18			
2009	**CACC**[3]										-0.087	**0.992**	0	-0.143	**0.967**	-0.346
	CPOOL[3]										**-0.990**	-0.075	0.111	**-0.980**	-0.167	-0.079
	SAL										0.114	0.106	**0.993**	0.136	-0.190	**-0.935**
	(% S)										34	46	20	78	15	7
2010	**CACC**[3]	-0.402	0	**0.872**				-0.269	**-0.957**	0.148	-0.365	**0.928**	0	-0.131	**0.991**	0.133
	CPOOL[3]	**-0.843**	-0.376	-0.472				**-0.963**	0.271	0	**-0.921**	-0.371	-0.160	**-0.973**	0.132	-0.209
	SAL	-0.357	**0.926**	0.132				0	0.104	**0.989**	-0.138	0	**0.987**	-0.191	0	**0.969**
	(% S)	60	31	9				49	39	12	34	46	20	37	46	16

[1] Positive coefficients on this factor indicate that the species was found in location with higher values than the average cell whilst negative coefficients indicate the opposite.

[2] Specialisation factors (S) one and two (S1 and S2), which indicate how narrow the range of conditions occupied by the species is (essentially conveying niche width). S will be > 0 whenever female seals were found to occupy a narrower range of conditions than was available across the study site; the higher this value (the greater the absolute value of the coefficient), the more restricted the females' range on the corresponding EGV.

[3] Avoidance of large values of 'cost-distance' to a feature (indicated by negative marginality coefficients) may be understood as a preference for proximity to this feature.

Table 4.3 EGV contributions to female global marginality and specialisation for each focal day. Absolute values only reported (signs unimportant to interpretation here). CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest contribution to each factor.

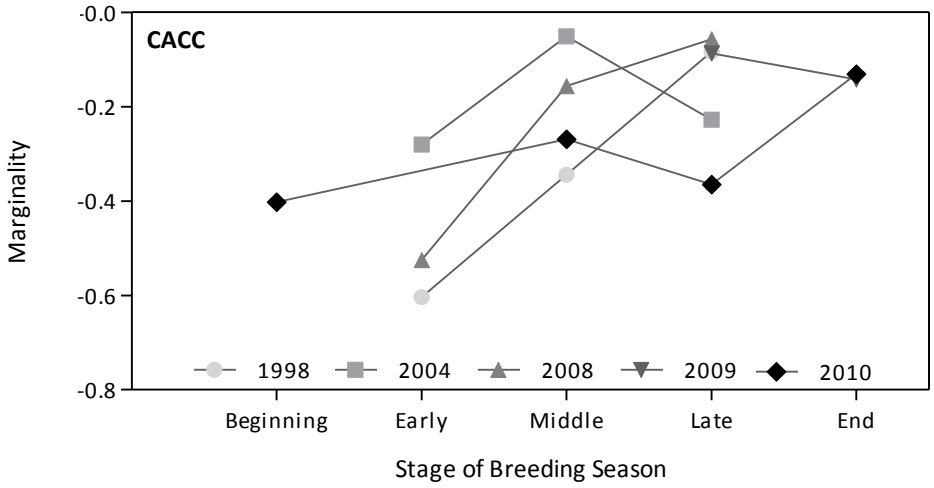
Stage of Breeding Season:		**Beginning**		**Early**		**Middle**		**Late**		**End**	
Year	**EGV**	**Margin-ality**[1]	**Special-isation**[2]	**Margin-ality**[1]	**Special-isation**[2]	**Margin-ality**[1]	**Special-isation**[2]	**Margin-ality**[1]	**Special-isation**[2]	**Margin-ality**[1]	**Special-isation**[2]
1998	**CACC**[3]			0.604	**3.102**	0.344	**3.450**	0.084	1.349		
	CPOOL[3]			**0.740**	2.519	**0.905**	3.338	**0.994**	**1.816**		
	SAL			0.296	2.837	0.248	3.340	0.076	1.724		
2004	**CACC**[3]			0.280	5.742	0.051	2.779	0.228	4.280		
	CPOOL[3]			**0.920**	**8.542**	**0.999**	**6.795**	**0.961**	**5.071**		
	SAL			0.276	4.279	0.007	1.287	0.158	4.144		
2008	**CACC**[3]			0.525	6.905	0.156	4.793	0.057	2.343		
	CPOOL[3]			**0.698**	4.641	**0.980**	3.730	**0.950**	**6.557**		
	SAL			0.488	**7.581**	0.123	**4.841**	0.308	5.566		
2009	**CACC**[3]							0.087	**2.491**	0.143	4.678
	CPOOL[3]							**0.990**	2.019	**0.980**	**13.305**
	SAL							0.114	1.460	0.136	3.275
2010	**CACC**[3]	0.402	35.111			0.269	5.416	0.365	**4.037**	0.131	**3.268**
	CPOOL[3]	**0.843**	**70.527**			**0.963**	**5.969**	**0.921**	3.770	**0.973**	2.836
	SAL	0.357	54.634			0.029	1.792	0.138	1.847	0.191	1.431

[1] Absolute values for EGV contributions to marginality have been reported; a higher marginality coefficient here indicates a greater contribution to overall marginality by that EGV.

[2] Specialisation factor, which indicates how narrow the range of conditions occupied by the species is (essentially niche width). S varies between 1 and infinity and will exceed unity whenever female grey seals were found to occupy a narrower range of conditions than was available across the study site; the higher this value, the more restricted the females' range on the corresponding EGV.

[3] Avoidance of large values of 'cost-distance' to a feature (indicated by negative marginality coefficients) may be taken as a preference for proximity to this feature.

A



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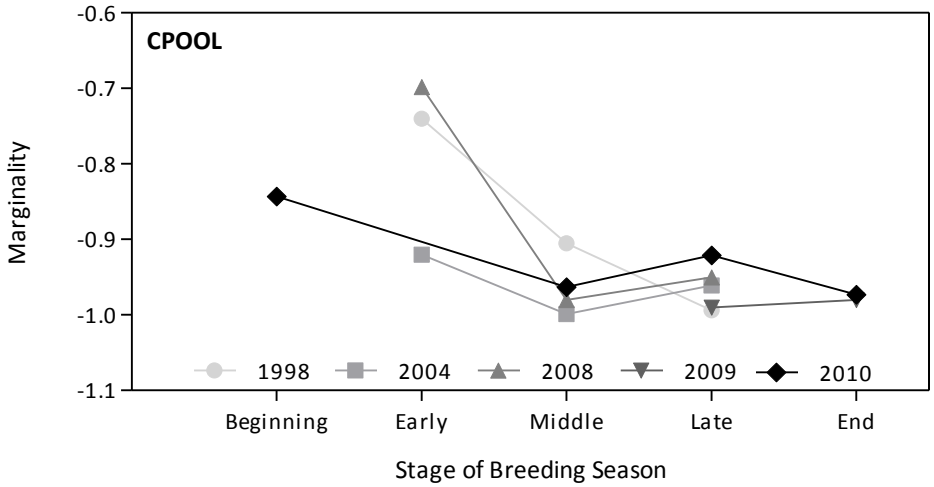

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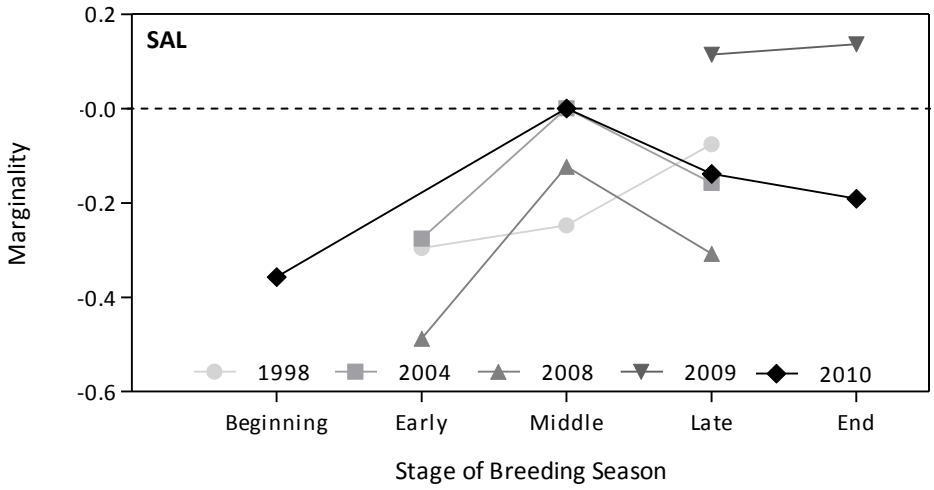

Figure 4.5: Change in female marginality coefficients for each EGV throughout all five breeding seasons. **A:** CACC; **B:** CPOOL; **C:** SAL. CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity.

4.3.2 Ecological niche of grey seal neonates

ENFA results indicate that grey seal neonates, similarly to adult females, tend to be found in areas in which conditions depart only moderately from the average available and are somewhat restricted in range relative to those which are available over the SS. This restriction in range is corroborated by the results presented in Chapter 3, which together show that neonates tend to be found in sites with intermediate values of each EGV. CPOOL is the EGV which contributes the most to neonate marginality, whilst the EGV that contributes the most to the specialisation is more variable between model runs (Section 4.3.2.3).

4.3.2.1 Marginality of neonate distributions

All neonate marginality values are greater than zero, though none exceed 0.5 (Table 4.4), indicating a tendency for neonates to be found in areas in which conditions depart only moderately from the SS mean. This is similar to the females, and is unsurprising given that neonate locations are primarily determined by female site choice. A comparison of Tables 4.1 and 4.4 shows that neonate marginality is typically lower than that of females, suggesting that females are found in areas in which conditions are further from the SS mean than are neonates. Given the preferences of females (Section 4.3.1), it is tempting to infer that females may leave pups in areas that are less 'preferred' by other females, which are likely to be more average in terms of overall conditions, at relatively higher CACC, CPOOL and salinity (Section 4.3.1). Females could then commute to more preferred areas, closer to pools of lower salinity (Section 4.4).

The overall neonate marginality is relatively low in all cases, though its variability within each season may be informative. Marginality generally decreases over the season, and is always lower at the end than that at the start of the season (Table 4.4 and Figure 4.6). Although most years show a consistent decrease in marginality across the season, there is an apparent discrepancy in 2008. In 2008 neonate marginality decreases between the early (0.408) and middle (0.319) stages before increasing again later in the season (though only to 0.350, a lower value than early in the season). However, this apparent discrepancy does not stand out amongst the values in the other years, which show a general trend for decreasing marginality over the season (Figure 4.6A). However, there was no significant relationship between breeding season stage and marginality across the five seasons, with no consistency in neonate marginality within breeding season stages (Randomisation Test, RSS = 0.028, p = 0.053). However, this does not imply that the change within each breeding season is non-significant, only that the marginality cannot be predicted by stage of breeding season. As with the adult females this is likely partly due to changes in EGVs between seasons, but may also be due to the fairly loose definition of 'stage' of breeding season. The decreasing marginality across most seasons suggests that as the season progresses neonates are found more frequently in areas with EGVs closer to the 'global' average

than at the beginning of the focal season. It may be that as more females come ashore, fewer females are able to stay both close to their pup *and* in their preferred conditions. Therefore a greater proportion of females may have to leave their pups in more average conditions, finding a trade-off between the risk of losing contact with the pup and the thermoregulatory benefit of proximity to pools. Another, though not mutually exclusive, explanation is that the SS as a whole tends to become wetter over the breeding seasons, so all sites become 'more average' in terms of CPOOL; neonate locations would then appear to become 'more average' even in the absence of changes in female pupping site preference. This appears to be the case for most seasons, excluding 2004 (Section 3.3); however, it is important to remember that ENFA accounts for global habitat use relative to availability, suggesting that there may be a real change in site use.

4.3.2.2 Specialisation of neonate distributions

The global neonate specialisation values are variable both within and across breeding seasons. However, unlike the specialisation scores for females, there does not appear to be a consistent trend in the direction of change across each season. For 1998, 2004 and 2008 there is an overall decrease between the early and late stages of the breeding seasons, though with some discrepancies (Table 4.4). However, it may be noted that in 1998 there is a similar trend as shown by the females, i.e. a seemingly anomalous (though very small) increase in specialisation between the early and middle stages of the breeding season, followed by an overall decrease in the late stage. The neonates also follow the same pattern as the females in 2008, with an increase in specialisation between the middle and late stages of the breeding season, though with an overall decrease between early and late 2008. The only other discrepancies are large increases in global specialisation between the late stage and end of the 2009 and 2010 seasons. However, unlike with the females, there is an overall increase in specialisation between the middle and end of the 2010 season.

Neonate tolerance is given more attention here due to ease of interpretation relative to specialisation. Neonate tolerance values are generally higher than those for females, possibly indicating a that neonates are less specialised and are found in sites with a wider range of EGV values than females. This seems logical as neonates at this stage of development, which have only a thin layer of subcutaneous blubber, are not likely to suffer thermal stress from overheating, and are therefore less dependent on proximity to pools than the females (Boily and Lavigne, 1996). The general increase in tolerance over each season (Table 4.4 and Figure 4.6C) appears to indicate that neonates occupy a narrower range of conditions earlier in the season than later in the season. This was supported by a randomisation test, which showed a significant relationship between breeding season stage and neonate tolerance (Randomisation Test, RSS = 0.028, p = 0.031). As neonates are not especially independent or mobile, this is likely a product of maternal

site choice. It may be that earlier in the season females can choose sites with good access both to pools and to the pups but as the season progresses the females may have to leave pups in less preferred areas and commute to the nearest pool. Later in the season this trade off may become less important as access to the typically more widespread pools is easier from a given pupping site. This reduction in the pup-pool trade off may also be promoted by a gradual reduction in the number of females ashore towards the end of the season, making the attainment of a site close to both pool and pups easier. However, there are some inconsistent values (e.g. late and end 2009); these will be explored in Section 4.3.2.3, considering EGV contributions to neonate specialisation.

Overall, these indices suggest that neonates occupy a relatively restricted range of sites that deviate from the average available. The changes in these indices over each season may be indicative of a change in female pupping site preferences, or of restricted choice later in the season. These trends are perhaps unsurprising, since the location of neonates will be mainly contingent upon the site choice of the females that show similar trends and preferences. This will be explored in greater depth in Section 4.3.2.3. Furthermore, there are a small number of inconsistent coefficients; this warrants further exploration in Section 4.3.2.3.

Table 4.4: Global marginality, specialisation and tolerance values for neonates on all 14 focal dates.

ENFA Output Type	Stage of Breeding	Year					
		1998	2004	2008	2009	2010	Average
Marginality	Beginning						
	Early	0.283	0.381	0.408			0.357
	Middle	0.279	0.334	0.319		0.408	0.335
	Late	0.133	0.285	0.350	0.249	0.332	0.270
	End				0.237	0.156	0.197
Specialisation	Beginning						
	Early	1.527	1.906	2.386			1.940
	Middle	1.531	1.762	1.658		1.660	1.653
	Late	1.305	1.799	2.193	1.227	1.491	1.603
	End				2.090	1.813	1.952
Tolerance	Beginning						
	Early	0.655	0.525	0.419			0.533
	Middle	0.653	0.568	0.603		0.602	0.607
	Late	0.766	0.556	0.456	0.815	0.671	0.653
	End				0.478	0.552	0.515

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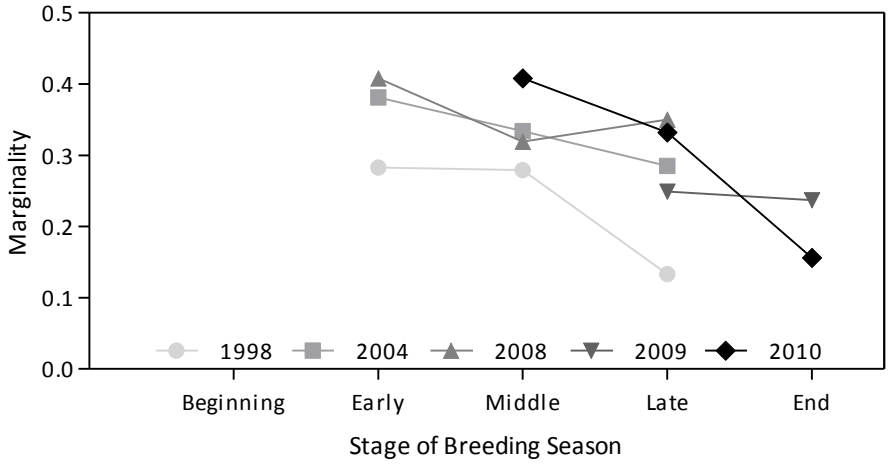

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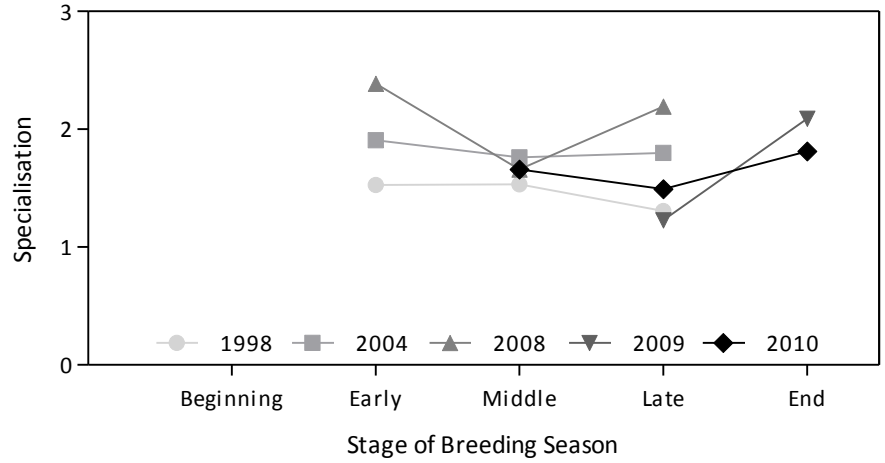

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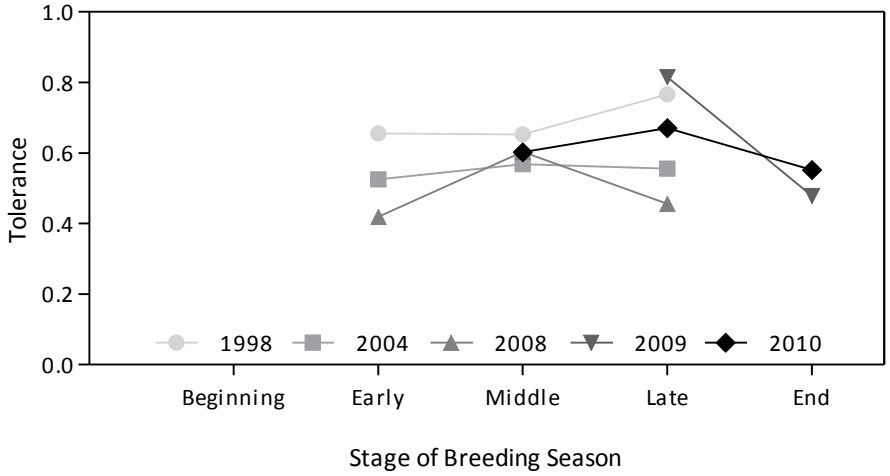

Figure 4.6: Change in neonate marginality, specialisation and tolerance throughout all five breeding seasons. **A:** Marginality; **B:** Specialisation; **C:** Tolerance (=1/Specialisation).

4.3.2.3 Determination of EGV preferences, and analysis of intra-seasonal change in preferences

All three EGVs were associated with neonate habitat 'selection', though each EGV contributes differently to the marginality and specialisation of the neonates between focal days. Table 4.5 shows the contribution of each EGV on the three factors for each focal day, and also provides information from the ENFA scores table, which replaces negligible coefficients with '0'. The three factors accounted for 100% of the total sum of eigenvalues (that is, 100% of the marginality and 100% of the specialisation) in all cases. The first (marginality) factor accounts for the total marginality and a certain percentage of the specialisation (indicated by '% S', Table 4.5), which is variable between model runs, ranging between 31% and 68% of total specialisation. The remaining specialisation is accounted for by the subsequent specialisation factors (S1 and S2).

The marginality coefficients for each EGV (Table 4.5 and Figure 4.7) demonstrate that neonates tended to be found in locations with lower EGV values than are available on average over the SS. This is perhaps unsurprising as females determine the initial location of each neonate, and show similar habitat affinities. The coefficients demonstrate that CPOOL contributes the most to neonate marginality. The only exception to this is at the end of the 2010 season, when the EGV contributing the most to marginality is salinity. All CPOOL marginality coefficients are negative and very large, indicating that neonates 'prefer' sites with much lower CPOOL than is available on average over the SS, with no consistent trend in change over the season. In the majority of cases salinity has the second largest marginality coefficient, though this is variable both between and within breeding seasons. The salinity marginality coefficients are typically negative or equivalent to zero (Table 4.5), and show that neonates tend to be found in locations with lower than average salinity, with no consistent change in preference over each season (Figure 4.7). In total, 10 of the 14 coefficients suggest a tendency for neonates to be found in locations with lower than average salinity, two suggest no preference and two (in 2009, similarly to the adult females) suggest a preference for higher than average salinity. This is explored further depth in Section 4.4. As with females, where the salinity marginality values are positive or equivalent to zero, the contribution of salinity to global specialisation is very low (Table 4.6), indicating that sites of higher salinity are only occupied when a wider range of values (a greater number of pupping sites) are occupied.

The CACC marginality coefficients for neonates also tend to be negative or equivalent to zero (Table 4.5), with only three exceptions to this (the final stage of the 1998, 2008 and 2010 seasons) and no consistent trend in change over each season (Figure 4.7). Furthermore, for three of the five seasons considered (1998, 2008 and 2010) there is a clear trend for an increasing preference for higher CACC values as the season progresses, generally beginning the season with a preference for lower CACC values than are available on average. A comparison of the EGV coefficients for females and neonates (Tables 4.2 and 4.5) indicates that neonates show the same

trend in CACC preference as females. This was somewhat expected given that a neonate's initial location is determined by the female, however it is interesting to note that 11 out of the 14 models suggest that higher values of CACC are more important for neonates than females on the same date. For example, in early 1998, the score tables give a -0.604 CACC coefficient for females and -0.389 for neonates, but later in the season a -0.084 and 0.050 respectively. This is supported by the findings in Chapter 3 (Section 3.3.4.2), which demonstrated that, where significant differences in female and neonate CACC values exist, neonates are generally found further from access than the females. This will be considered further in Section 4.3.3.

The EGV specialisation coefficients indicate how restricted the neonate range is on the corresponding EGV, and here demonstrate neonate use of a restricted range of each EGV. The specialisation factors each account for a large proportion of the observed specialisation (Table 4.5; mean = 28.3, minimum = 9) and a degree of specialisation on all EGVs is seen on at least one of the specialisation factors on each focal day. CPOOL consistently appears to have the *lowest* absolute specialisation values on the S1 and S2 factors; however this is misleading because a large proportion of the specialisation is accounted for by the marginality factor. In fact, CPOOL not only contributes the most to marginality in all cases but also contributes the most to specialisation in over half of the cases (Table 4.6). This demonstrates that neonates typically occupy sites with a restricted range of CPOOL values that differ from the average over the site. Tables 4.5 and 4.6 demonstrate that CACC and salinity both contribute considerable amounts to neonate specialisation, indicating a tendency to also occupy sites with a restricted range of these EGVs. This is supported by the findings from Chapter 3 (Section 3.3.4.2 and 3.3.4.3), which indicated that neonates typically avoid the extreme high and low CACC and salinity values.

It is, therefore, clear that neonates are essentially linked to a relatively restricted range of EGVs in sites closer than the average location to pools, which are typically of a lower salinity than is available on average over the SS. There is an overall preference for these sites to be located farther from access points relative to the females. Integration of these results with those from Chapter 3 shows that neonates tend to be found at sites with intermediate EGV values that are lower than the SS average. No consistent trends in neonate EGV preferences are apparent throughout each season, though the global marginality and tolerance indicate that neonates are found in increasingly 'average' conditions and are typically less specialised later in each season. The trend in tolerance values indicates that neonate niches typically widen over the season, suggesting that females may be leaving their pups in more 'average' locations less favoured by the females as the season progresses, whilst the females themselves still opt for more marginal conditions, especially regarding CPOOL. This has been considered further in Section 4.3.2.2.

Table 4.5: Coefficients of EGVs on each ENFA factor for grey seal neonates for each focal day. The marginality factors explain 100% of the marginality and a certain amount of specialisation. '%S' indicates the amount of specialisation (S) accounted for by each factor. Bold numbers indicate the EGV with the largest contribution to each factor. CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity.

Stage of Breeding Season:		Beginning			Early			Middle			Late			End		
Year	**EGV**	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]	**Margin-ality**[1]	**S 1**[2]	**S 2**[2]
1998	**CACC**[3]				-0.389	0.272	**0.844**	-0.145	0.385	**-0.878**	0.050	**-0.982**	-0.034			
	CPOOL[3]				**-0.853**	0.256	-0.481	**-0.937**	0.242	0.270	**-0.998**	-0.045	-0.026			
	SAL				-0.349	**-0.928**	0.235	-0.318	**-0.890**	-0.395	0	-0.182	**-0.999**			
	(% S)				38	44	18	44	35	21	36	35	29			
2004	**CACC**[3]				-0.147	**0.924**	-0.470	0.063	**0.529**	0.804	-0.272	-0.310	**0.874**			
	CPOOL[3]				**-0.958**	-0.044	0.287	**-0.991**	0.135	**-0.021**	**-0.919**	-0.198	-0.360			
	SAL				-0.246	-0.380	**-0.835**	-0.120	-0.838	0.594	-0.286	**0.930**	0.326			
	(% S)				61	22	16	50	30	20	39	37	24			
2008	**CACC**[3]				-0.127	0.188	**-0.995**	0	**0.938**	-0.430	0.401	0.168	**0.914**			
	CPOOL[3]				**-0.879**	0.434	0.234	**-0.997**	0.035	0.058	**-0.870**	-0.237	0.401			
	SAL				-0.460	**-0.881**	-0.184	-0.070	-0.345	**-0.901**	-0.286	**0.957**	0.060			
	(% S)				45	36	19	33	40	27	44	46	9			
2009	**CACC**[3]										-0.149	**0.988**	-0.169	-0.220	0.060	**-0.969**
	CPOOL[3]										**-0.955**	-0.152	-0.231	**-0.972**	0.064	0.210
	SAL										0.256	0	**-0.958**	0.076	**0.996**	-0.129
	(% S)										31	50	19	68	17	15
2010	**CACC**[3]							-0.298	**-0.953**	0.083	-0.197	**0.977**	0.064	0.174	**0.951**	-0.240
	CPOOL[3]							**-0.953**	0.294	-0.090	**-0.980**	-0.199	0	-0.609	-0.099	**-0.788**
	SAL							-0.062	0.070	**0.992**	0	0.078	**0.997**	**-0.774**	0.292	0.567
	(% S)							33	48	19	43	37	19	40	35	24

[1] Positive (negative) values for this factor indicate that the pups were found in location with higher (lower) values than the average cell.

[2] Specialisation factors (S), which indicate how narrow the range of conditions occupied by the neonates is (essentially niche width). S will be > 0 whenever the pups occupied a narrower range of conditions than was available across the study site; the higher this value (the greater the absolute value of the coefficient), the more restricted the neonate's range on the corresponding EGV.

[3] Avoidance of large values of 'cost-distance' to a feature (indicated by negative marginality coefficients) may be taken as a preference for proximity to this feature.

Table 4.6 EGV contributions to neonate global marginality and specialisation for each focal day. Absolute values only reported (signs unimportant to interpretation here). CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity. Bold numbers indicate the EGV with the largest contribution to each factor.

Stage of Breeding Season:		**Beginning**		**Early**		**Middle**		**Late**		**End**	
Year	**EGV**	**Margin-ality**[1]	**Specia-lisation**[2]	**Margin-ality**[1]	**Specia-lisation**[2]	**Margin-ality**[1]	**Specia-lisation**[2]	**Margin-ality**[1]	**Specia-lisation**[2]	**Margin-ality**[1]	**Specia-lisation**[2]
1998	**CACC**[3]			-0.389	4.076	-0.145	**3.767**	0.050	**1.893**		
	CPOOL[3]			**-0.853**	3.652	**-0.937**	3.901	**-0.998**	1.979		
	SAL			-0.349	**2.950**	-0.318	2.674	-0.024	1.835		
2004	**CACC**[3]			-0.147	4.063	0.063	**3.292**	-0.272	4.189		
	CPOOL[3]			-**0.958**	**7.026**	**-0.991**	5.000	**-0.919**	5.036		
	SAL			-0.246	4.056	-0.120	4.023	-0.286	**5.168**		
2008	**CACC**[3]			-0.127	5.177	0.011	4.081	0.401	4.921		
	CPOOL[3]			**-0.879**	10.221	**-0.997**	2.978	**-0.870**	**7.696**		
	SAL			-0.460	**9.577**	-0.070	**3.306**	-0.286	8.299		
2009	**CACC**[3]							-0.149	**2.594**	-0.220	**4.037**
	CPOOL[3]							**-0.955**	1.876	**-0.972**	9.215
	SAL							0.256	1.189	0.076	3.126
2010	**CACC**[3]					-0.298	**4.736**	-0.197	**3.087**	0.174	**4.576**
	CPOOL[3]					**-0.953**	3.902	**-0.980**	3.391	-0.609	4.661
	SAL					-0.062	2.001	-0.034	1.572	**-0.774**	5.459

[1] Absolute values for EGV contributions to marginality have been reported; a higher marginality coefficient here indicates a greater contribution to overall marginality by that EGV.

[2] Specialisation factor, which indicate how narrow the range of conditions occupied by the neonates is (essentially niche width). S varies between 1 and infinity and will exceed unity whenever neonates occupy a narrower range of conditions than was available across the study site; the higher this value, the more restricted the pup's range on the corresponding EGV.

[3] Avoidance of large values of 'cost-distance' to a feature (indicated by negative marginality coefficients) may be taken as a preference for proximity to this feature.

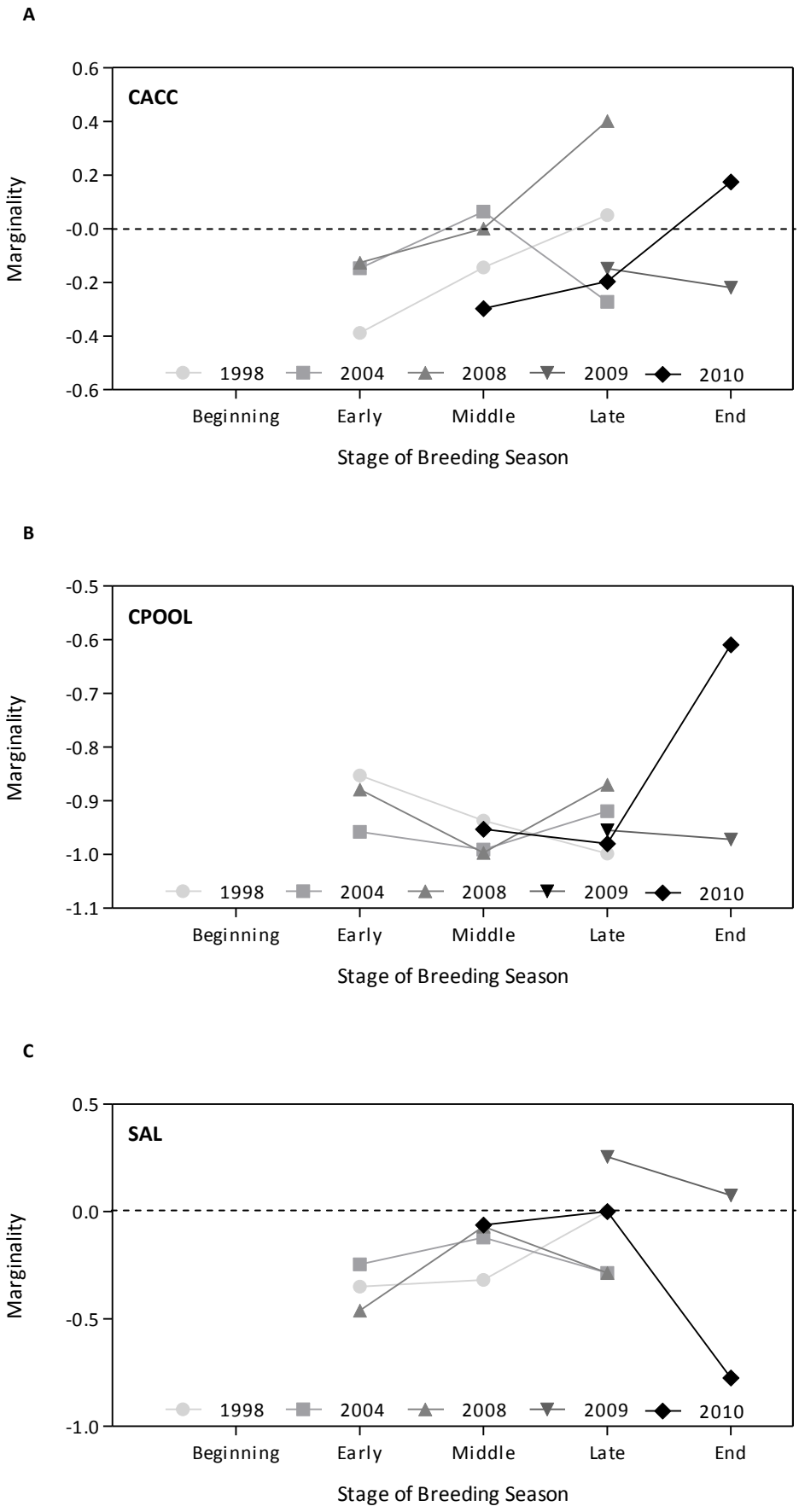

Figure 4.7: Change in neonate marginality coefficients for each EGV throughout all five breeding seasons. **A:** CACC; **B:** CPOOL; **C:** SAL. CACC = 'Cost-distance' to nearest access; CPOOL = 'Cost-distance' to nearest pool; SAL = Salinity.

4.3.3 Niche differentiation between females and neonates

Discriminant analysis was used to assess niche differentiation between females and neonates. However, it was impossible to interpret the DA results as the female and neonate distributions on the discriminant factor were highly overlapping on all focal days and, therefore, indistinguishable as positive or negative 'age classes'. Pianka's Overlap Index, *O*, confirms this high degree of overlap on all EGVs on all focal days (Table A3.1, Appendix 3; $O > 0.85$ in the majority of cases, and $O > 0.75$ in all cases). Overlap was typically lowest on the EGV CACC, suggesting that female and neonate niches differ most in terms of the CACC of occupied sites; indeed, all *O* scores lower than 0.860 are on this EGV (Table A3.1, Appendix 3). This is a result of neonates typically being found at higher elevations and further from access than adult females (Section 3.3.4).

4.3.4 ENFA-derived habitat suitability values

HS model cross-validation indicated that female models typically perform better than neonate models (Table A3.2). These differences in model accuracy may highlight the different behavioural choices leading to female habitat *versus* pupping site preferences. If females do indeed leave pups in generally more average conditions, the pups are less likely to be particularly associated with particular values of any EGVs, making the HS model generally more difficult to predict accurately, as reflected in the CBI results. This makes biological sense as the females have ecological 'needs' (for example, for proximity to pools), whereas neonates typically only require sufficient maternal attention. It is unlikely that the differences in model accuracy are simply a product of the larger sample sizes in females relative to neonates as previous studies focusing on interspecific differences in habitat preferences have shown that model precision and reliability are not improved by inclusion of a higher number of presence points (Zaniewski *et al.,* 2002; Sattler *et al.,* 2007). Also, the HS models generally perform better earlier than later in each season (excluding 2008), indicating that the distribution of individuals in areas of high and low HS is generally more random relative to the EGV distributions later in the season. It is possible that the number of individuals ashore influences this, as when more individuals are ashore proportionally fewer will be able to acquire high suitability habitat; this is potentially indicative of preferential colonisation of higher suitability areas by the first females ashore and will be discussed in Section 4.4. Despite the variable model performance, the HS maps (e.g. Figure 4.8) corroborate the distribution of high and low suitability areas anticipated by long-term researchers on North Rona (PPP and SDT, *pers. comm.*), indicating generally good performance at a broad, SS-wide scale.

The SS HS values are highly variable both within and between seasons, with higher average suitability occurring later in each season (except 1998 and 2009; Figure 4.9). On all focal dates, female and neonate locations have a median HS score of approximately 50, with considerable variation around this average (Figure 4.9), though female and neonate HS

distributions do not differ either from each other or between focal dates (Figure A3.1). On all focal dates, female and neonate locations show considerably higher HS than the SS average (Figure 4.9). MULTCOMP tests comparing female and global HS values with indicate significant differences in all cases, showing that females (and, by extension, pups) are found at higher suitability sites (Table 4.7) than are typically available on average over the SS.

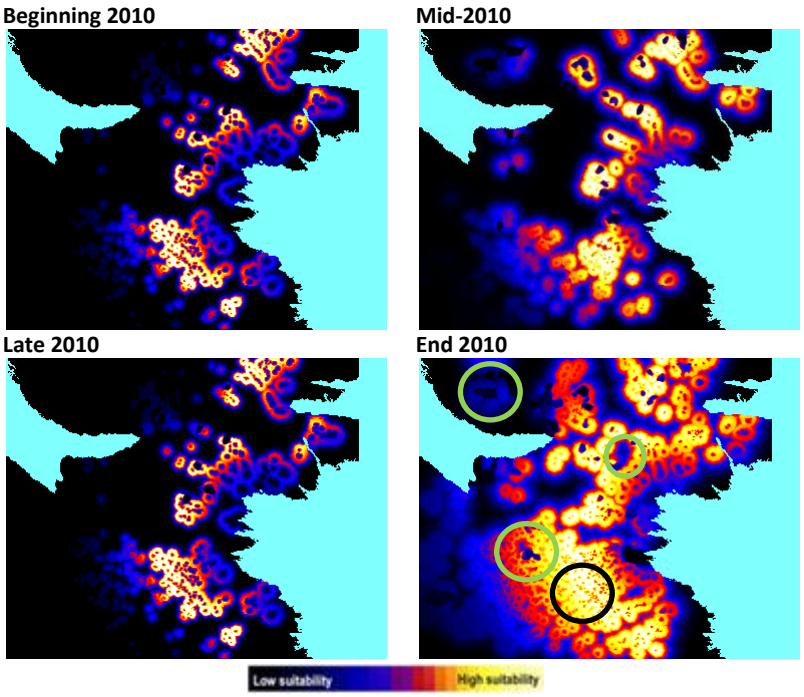

Figure 4.8: Habitat suitability maps for females during the 2010 breeding season. Additional maps not shown due to the general similarity across seasons and between age classes. Areas of highest suitability clearly have intermediate proximity to access points and pools of low salinity. More saline pools (example circled in green, End 2010) are clearly less suitable than those of lower salinity (circled in black, End 2010).

All HS maps are similar in terms of regions of high *versus* low suitability (e.g. Figure 4.8). Figure 4.8 shows that the highest suitability areas are at intermediate distances from pools (though not in the pools themselves, which show much lower suitability and produce darker patches within areas of high suitability on Figure 4.8). Figure 4.8 also demonstrates that not all pools are of equal suitability: those at intermediate distances to access points are most suitable for both females and neonates, whilst pools too close or far from access, or of high salinity, show diminished suitability (Figure 4.8). a comparison of the HS maps and the seal presence (observation) maps show that occasionally there are areas which are predicted to have high HS based on the distribution of EGVs, despite there being no individuals observed in that area (Figure 4.10). This is a product of the predictive, extrapolative nature of the SDM process and the lack of observations in these areas is likely due to historical colonisation processes and the fact that this is a declining colony; if the population was larger it seems likely (especially given the dispersive nature of the females identified in Section 3.3.3) that these highly suitable areas would also become colonised over time.

On all focal dates, the same EGVs are clearly important in determining HS of particular regions within the SS, and HS clearly varies at a very fine scale (Figure 4.8). As each season progresses, there is clearly some variation in the distribution of high and low suitability habitats between breeding season stages (Figure 4.8); however, areas of high/low suitability in one part of the season are typically of similarly high/low quality respectively in the next stage of the season. This is demonstrated by the high degree of positive correlation in HS values of each $1m^2$ raster grid cell between consecutive stages of each season (Table 4.8). Similarly, there is a high degree of correlation when stages of the breeding season are analysed for inter-annual variability. This showed that, for example, the early stage of 1998 is highly positively correlated with the early stage of 2004 and 2008 and with the beginning of 2010. The same was true of all stages compared across years; Table 4.9 demonstrates the correlations assessed. These correlations are marginally weaker than those for within-season changes in the HS of the SS, but demonstrate that many locations are consistent in their suitability between years.

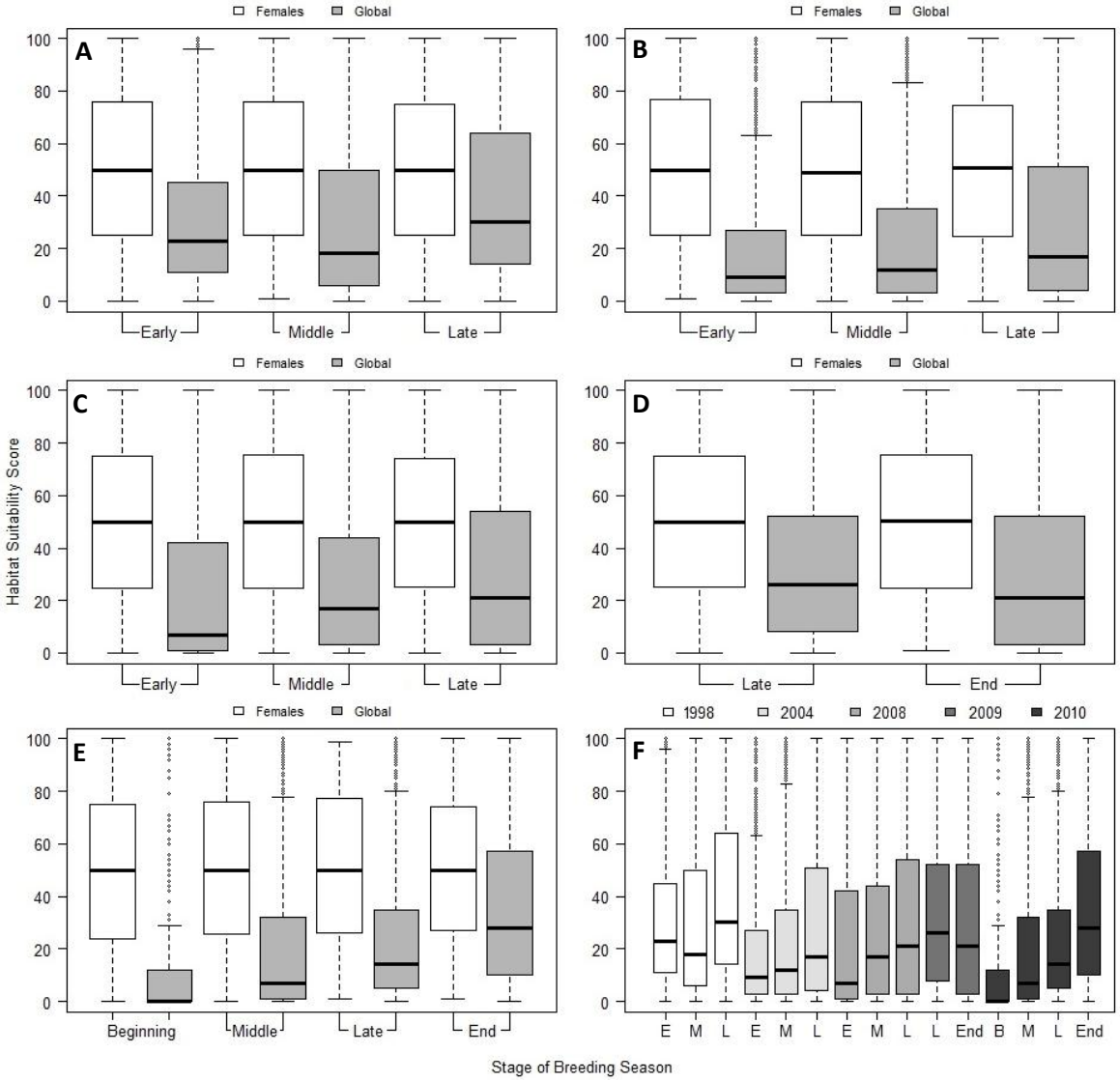

Figure 4.9: Female and global habitat suitability scores for all years. **A:** 1998; **B:** 2004; **C:** 2008; **D:** 2009; **E:** 2010; **F:** Global habitat suitability values for all seasons; "B"=Beginning, "E"=Early, "M"=Mid, "L"=Late. HS scores for neonates not presented as these are indistinguishable from female scores (Figure A3.1).

Table 4.7. Results of MULTCOMP tests assessing the difference between female and global HS distributions on each focal day. All differences are significant at α = 0.001. MULTCOMP tests were performed on HS values that had been shifted (by +1) and square root-transformed, data presented are untransformed.

Year	Stage	Female Mean	Female SD	Global Mean	Global SD	F	*p*
1998	Early	50.1	29.0	30.5	25.1	-12.22	< 0.001
	Mid	50.3	29.1	29.4	27.7	-15.91	< 0.001
	Late	50.1	28.9	38.3	28.5	-8.78	< 0.001
2004	Early	50.4	29.3	20.0	24.6	-15	< 0.001
	Mid	49.9	28.9	22.2	25.7	-18.36	< 0.001
	Late	50.0	29.1	29.4	29.9	-12.65	< 0.001
2008	Early	50.0	28.9	24.7	30.0	-15.13	< 0.001
	Mid	50.2	29.0	26.2	27.4	-14.27	< 0.001
	Late	50.1	28.9	30.9	31.0	-11.07	< 0.001
2009	Late	50.1	28.9	32.7	28.0	-8.75	< 0.001
	End	50.1	29.1	29.8	29.4	-8.98	< 0.001
2010	Beginning	51.0	30.3	11.3	21.8	-15.87	< 0.001
	Mid	50.6	29.2	19.0	25.0	-13.28	< 0.001
	Late	50.5	29.4	24.8	25.6	-6.08	< 0.001
	End	50.1	29.0	35.1	28.9	-11.73	< 0.001

Table 4.8: Results of the Pearson's product-moment tests for correlation in habitat suitability for all locations on the SS between stages of each breeding season. All tests were performed on global habitat suitability data shifted (by addition of a constant; +1) and square-root transformed for normality.

Year	Comparison	Correlation Coefficient	*t*	*p*
1998	Early – Mid	0.739	314.19	< 0.001
	Mid – Late	0.662	253.59	< 0.001
2004	Early – Mid	0.710	288.82	< 0.001
	Mid – Late	0.770	346.31	< 0.001
2008	Early – Mid	0.719	296.28	< 0.001
	Mid – Late	0.625	229.63	< 0.001
2009	Late – End	0.689	272.47	< 0.001
2010	Beginning – Mid	0.683	268.05	< 0.001
	Mid – Late	0.693	275.26	< 0.001
	Late – End	0.688	272.13	< 0.001

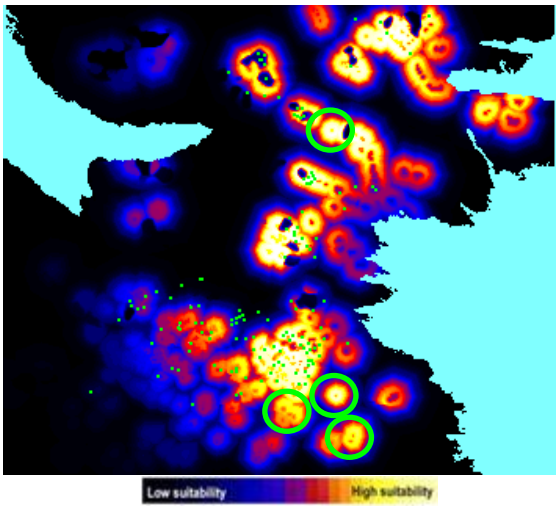

Figure 4.10: Overlay of female presences (green points, enlarged (×4) for clarity) on North Rona on 12/10/2010 on the habitat suitability map computed using ENFA for Mid-2010. Examples circled in green indicate the areas predicted to have high suitability despite a lack of species presence.

Table 4.9: Results of the Pearson's product-moment tests for correlation in habitat suitability at all locations on the SS for each stage between breeding seasons. All tests were performed on global habitat suitability data shifted (by addition of a constant; +1) and square-root transformed for normality.

Stage	Comparison	Correlation Coefficient	*t*	*p*
Early/Beginning	**1998 – 2004**	0.638	237.84	< 0.001
	1998 – 2008	0.693	275.97	< 0.001
	1998 – 2010	0.618	225.62	< 0.001
	2004 – 2008	0.699	280.52	< 0.001
	2004 – 2010	0.713	291.87	< 0.001
	2008 – 2010	0.664	254.64	< 0.001
Mid	**1998 – 2004**	0.673	261.16	< 0.001
	1998 – 2008	0.806	389.89	< 0.001
	1998 – 2010	0.665	255.20	< 0.001
	2004 – 2008	0.770	345.76	< 0.001
	2004 – 2010	0.706	286.00	< 0.001
	2008 – 2010	0.773	349.52	< 0.001
Late	**1998 – 2004**	0.813	401.05	< 0.001
	1998 – 2008	0.739	314.27	< 0.001
	1998 – 2009	0.726	302.28	< 0.001
	1998 – 2010	0.665	255.46	< 0.001
	2004 – 2008	0.722	298.89	< 0.001
	2004 – 2009	0.761	316.33	< 0.001
	2004 – 2010	0.741	316.33	< 0.001
	2008 – 2009	0.612	221.62	< 0.001
	2008 – 2010	0.615	223.70	< 0.001
	2009 – 2010	0.662	253.04	< 0.001
End	**2009 – 2010**	0.777	353.58	< 0.001

4.4 Discussion

This chapter, in conjunction with Chapter 3, has demonstrated that females exhibit preferences in their choice of both pupping site and subsequent habitat, if the assumption is accepted that neonate locations indicate the locations chosen by females as pupping sites. In both cases, the 'niche' can be described well, with a fairly high degree of predictive accuracy, in terms of three key EGVs: 'cost-distance' to access, 'cost-distance' to pools and salinity. Exploratory analysis (Chapter 3) and ENFA indicate that in both cases, females prefer sites with intermediate values of these three key EGVs, typically avoiding extreme values and tending to inhabit areas with EGV values less than the 'global' average. This confirms previous observations that pool availability is an important determinant of female distribution (Boyd *et al.,* 1962; Anderson *et al.,* 1975; Pomeroy *et al.,* 2000a; Twiss *et al.,* 2000a, 2002, 2007; Redman *et al.,* 2001) and supports those assertions that proximity to access is important, with females initially aggregating around access points (Pomeroy *et al.,* 1994), but that females likely prefer sites that are not directly next to these areas, rarely pupping within 10m of an access point (Twiss *et al.,* 2003; Stephenson *et al.,* 2007). The increased cost of locomotion implicit in reaching sites with high CACC values probably contributes to this, whilst it is likely that sites with low CACC are avoided due to the potential for trampling of pups in these areas by the 'traffic' associated with adults joining or leaving the colony (Twiss *et al.,* 2003; Stephenson *et al.,* 2007). This may also explain why neonates were typically found in sites with intermediate CPOOL: neonates nearer to pools, around which there are higher aggregations of females and frequencies of locomotion and aggressive behaviour (PPP and SDT,

pers. comm.), would be in greater danger than if they were further away. It is likely that females, on average, also 'prefer' sites with intermediate CPOOL due to the need to attend to the pup, which is typically not directly next to a pool, and simply commute to pools as required (Redman *et al.,* 2001). Female avoidance of pools, reflected in the low suitability of pool locations seen in Figures 4.2, 4.8 and 4.10, may also be associated with an avoidance of aggressive interactions with more dominant, possibly older or more experienced, females who may monopolise access to these pools (Twiss *et al.,* 2000, 2002).

Much recent research has demonstrated the direct effects of temperature on spatial behaviour, habitat selection and population dynamics in a range of organisms, from ectotherms to endotherms (Walther *et al.,* 2002; Parmesan, 2006; Aublet *et al.,* 2009; Bowyer and Kie, 2009; Bourgoin *et al.,* 2011; Hansen *et al.,* 2011). Grey seals, with their large body size and effective blubber layer insulation, are well adapted to life in a cold marine environment and are in a "thermoneutral zone" between around -10 and 23°C (Folkow and Blix, 1987; Hansen and Lavigne, 1997); this approximates the range of temperatures in which an individual can survive whilst maintaining a relatively constant metabolism. This has been understood as a limit on the northern range of the grey seal, which is restricted by colder temperatures further north, whilst the autumn air temperatures at breeding sites were assumed not to challenge the upper limit of the thermoneutral zone (Hansen and Lavigne, 1997). However, it has been found that the adaptations of grey seals to cold temperatures also leave them prone to thermal stress from overheating whilst hauled out to breed (Twiss *et al.,* 2002), especially as the basal metabolic rate (BMR) during lactation is typically approximately 2.3 times the 'normal' BMR (Reilly *et al.,* 1996). Phocids are unable to pant or sweat (Riedman, 1990) and cooling whilst hauled out is achieved by thermal radiation (Øritsland *et al.,* 1978), mainly through 'thermal windows', which are poorly insulated areas such as the flippers to which blood is shunted to enhance radiative heat dissipation (Ronald *et al.,* 1977). This is likely to be most effective at night, when there is no solar radiation to warm the blood in peripheral vessels at the surface of the skin. However, during warm days it appears that radiative heat loss is not sufficient to prevent thermal stress by overheating (Twiss *et al.,* 2002), generating a requirement for behavioural thermoregulation, for example by bathing in pools of water (Twiss *et al.,* 2002); this is also common in other pinnipeds in temperate and warm climates (Gentry, 1973; Campagna and Le Beouf, 1988). However, despite identifying proximity to pool as important for grey seal site use, this study failed to find a link between female and neonate CPOOL and either temperature or rainfall (Chapter 3). Given previous evidence, this is likely due to insufficient data. This study analysed 15 focal days, giving a small sample size of 15 daily temperatures and four focal days of rainfall data. Furthermore, the 15 focal dates varied in terms of pool availability, local seal density and variance in hourly temperature, relative humidity and rainfall, all of which are likely to affect the need for, or ability of, seals to maintain close proximity to pools. The evidence also suggests that pools are used for drinking as well as

thermoregulation; although local weather *may* influence the water balance of female seals, the main influence on water balance is likely to be the burden of lactation, which may explain why no clear link between pool use and local weather is apparent. Furthermore, the relationship between rainfall and proximity to pool is likely to be complex: due to the geology of the SS increased rainfall results in more extensive pool coverage (SDT, *pers. comm.*). Following rainfall, an abundance of pools means that females will likely be closer to a pool, however, it may be that the need for behavioural thermoregulation is reduced due to the cooling effect of evaporative heat loss from wet pelage (McCafferty *et al.,* 2005). Such microclimatic effects will become increasingly important for many species, including the grey seal, as the climate becomes increasingly variable (Jenkins *et al.,* 2009). It is important to continue to assess these at this fine spatial and temporal scale, as their impacts on animal behaviour are typically most pronounced when assessed in this way (Loe *et al.,* 2007; Aublet *et al.,* 2009; van Beest *et al.,* 2011), though a more complex modelling approach than that utilised here would be necessary to tease apart to various effects of climate, topography and (water) resource availability on seal distribution and behaviour. Coarser measurements of climatic change are better suited to assessing broad scale range shifts (e.g. Walther *et al.,* 2002) than to fine spatial scale behavioural studies (e.g. Twiss *et al.,* 2002; 2007).

Quantifying the effects of temperature and pool availability on the thermoregulatory and spatial behaviour of the focal species is important as a preliminary to understanding the impacts of climate and topography on population dynamics (Grosbois *et al.,* 2008; Mysterud and Saether, 2011). This understanding is critical because behavioural and spatial adjustments are likely to involve trade-offs (Sih, 1980; Hamel and Cote, 2008) that could influence broader aspects of grey seal ecology (Twiss *et al.,* 2000a). For example, the trade-off between proximity to pool and proximity to pup directly influences the level of maternal attendance and investment in pups (and therefore pup mortality; Redman *et al.,* 2001; Twiss *et al.,* 2000a; 2003), whilst a requirement for proximity to pools has been shown to affect the opportunity for sexual selection through influences on the environmental potential for polygamy (Twiss and Thomas, 1999; Twiss *et al.,* 2007). Given that the 'normal' degree of polygyny is based on mate monopolisation by dominant, higher quality males, a change in degree of polygyny may affect the overall quality of pups born via impacts on the genetic structure of the population. The preferences for habitat *versus* pupping site conditions shown by females indicates a potential trade off. Pupping sites tend to be relatively close to pools, though somewhat further than female locations. It is likely that being nearer to pools is more risky for pups, but being too far away increases the time and energy spent by the female in locomotion between the pup and the pool. This reduces the energy available for pup provisioning and places the pup in danger from conspecifics or predators during times of separation, and may increase the likelihood of permanent separation and pup starvation (Redman *et al.,* 2001). The response to any trade-offs, such as that discussed here, will likely vary between individuals (McNamara and Houston, 1996), though it is possible that individual females will react

consistently to changing conditions (Twiss *et al.,* 2012); this is discussed in detail in Section 6.4.3.

In some cases, behavioural adjustments in response to changing conditions do not involve a substantial trade-off (Pierce *et al.,* 2004), for example, during or immediately following periods of heavy rain on North Rona, when pools are abundant and females do not have to commute a great distance from their pup for access to water (Redman *et al.,* 2001). However, where this trade-off does occur access to water can prove to be more important than the risk of reproductive failure. During dry spells on North Rona, the requirement for proximity to water results in increased rates of female locomotion towards pools and less time spent close to pups (Redman *et al.,* 2001). This occurs despite the increased costs of aggression associated with locomotion through areas of high female density (Caudron, 1998; Twiss *et al.,* 2000a) and the higher risk of mother-pup separation which can result in pup starvation and death, or injury from conspecifics through trauma (i.e. trampling) or bites which can result in death directly or via infection (Anderson *et al.,* 1975, Baker and Baker, 1988; Pomeroy *et al.,* 1994; Redman *et al.,* 2001). This highlights the importance of the variability in local weather in determining the outcomes of behavioural and spatial adjustments. It would be interesting to assess whether the pup-pool trade-off is affected by the declining population size at North Rona. If this decline eventually led to lower breeding densities, females may (a) pup near to pools and reduce the trade-off, (b) commute but perhaps experience fewer aggressive interactions and therefore have more energy for investment in the pup or their own maintenance (Boness *et al.,* 1995; Pomeroy *et al.,* 1999), though potentially leave the pup more exposed to predation by gulls (typically greater black-backed gulls, *Larus marinus*) in lower density areas (SDT *pers. comm.;* Twiss *et al.,* 2003).

Given the influence of behavioural thermoregulation and therefore temperature on space use and ecological requirements of female grey seals, it is interesting to question whether the foraging abilities of females affects their distribution on the colony. Better foragers are likely to be in better body condition than other females, having developed a thicker blubber layer throughout the year (Pomeroy *et al.,* 1999). Given the intense insulative capacity of this blubber, better foragers may have increased requirements for access to pools for thermoregulation whilst on land. This could be addressed by direct observations of proximity to pool of individuals of varying body condition, which may be assessed directly by in-field weighing and indirectly through photogrammetry (Twiss *et al.,* 2000b). Observational studies could also assess any differences in requirement for proximity to pools between early and late lactation in individual females. Females lose an average of 82kg during lactation, equivalent to 46.5% of their body mass (Pomeroy *et al.,* 1999). This mass loss occurs mostly through blubber depletion, with very little protein catabolism (Goodman *et al.,*1980; Reilly, 1991; Cherel *et al.,* 1992; Arnould *et al.,* 2001; Noren *et al.,* 2003), and may influence the relative thermoregulatory requirements of individuals throughout lactation. Individual females may therefore have decreased requirements for proximity to pool as

their lactation progresses, due to loss of their insulative blubber. Such an investigation was beyond the scope of this research, though the ENFA suggested a possible effect of this, with females typically expressing less of a preference for proximity to pools as the season progresses; this may be a result of the fact that, generally speaking, females on the colony later in the season tend to be thinner than those that breed earlier (Fedak and Anderson, 1982; Pomeroy *et al.,* 1999; Twiss *et al.,* 2000a). To investigate this more thoroughly, data would be required on proximity to pool and body mass and/or composition throughout lactation for individually identified females, in addition to fine scale weather data to tease apart the effects of body condition, proximity to pool, adult female density, temperature, rainfall and possibly wind speed. It is also worth noting that the relationship between proximity to pool and stage of lactation is likely to be very complex, dependent not only upon the availability of pools and maternal condition but also on pup age; fatter, early lactation females may be inclined to stay with their young pup due to its vulnerability, whilst thinner females in late lactation may be more able to briefly abandon their less vulnerable pup to commute to a pool.

Female preference for intermediate EGV values may explain why we do not see a unidirectional change in EGV usage (i.e. towards pupping closer to pools) as the colony declines and fewer individuals compete for preferred sites. As individuals are not necessarily looking for the lowest possible 'cost-distance' to pools and access, rather than a unidirectional change in EGV usage with colony decline, we might expect to see a reduction in overall realised niche width as a larger proportion of individuals can acquire preferred sites and fewer have to choose sites with more 'extreme' EGV values. However, it is possible that the colony has not declined sufficiently to eliminate competition for preferred sites, so reduction in niche width may still be minimal. Interestingly, the preference for intermediate values corresponds to a basic tenet of niche theory: that the HS or fitness associated with a site does not have a monotonic relationship with EGVs at this site, but is likely to be represented by a continuous probability distribution, with decreasing HS or fitness either side of an 'optimum'. ENFA is therefore an ideal modelling approach in this instance as, unlike regression techniques, it does not assume linear, monotonic relationships between predictor (EGV) and response (presence) variables. Instead, ENFA accounts for non-linear relationships and describes the species' marginality and specialisation, two key measurements of the species' niche which relate directly to the shape of the continuous distribution describing resource use.

Overall, as the season progresses females and neonates are found in locations with EGV values closer to the SS average (they become less marginal). There are multiple potential, though not necessarily mutually exclusive, explanations for this. As CPOOL contributes so much to female and neonate marginality (Section 4.3.1.3 and 4.3.2.3), it is possible that a global decrease in CPOOL consistent with increasingly wet conditions on the colony over each season means that the

SS as a whole appears more 'average' as there are fewer areas that are far from pools. Females and neonates would, therefore, be expected to be found in sites with CPOOL values close to the SS mean, as these are more abundant. The results from Chapter 3 support this, showing that the global availability of EGVs changes within a season. However, ENFA assesses site use relative to the global availability of EGVs, so the change in EGV availability is taken into account, suggesting that the changes in marginality are at least partly due to changes in female site choice.

This change in site choice may be a result of preferential colonisation of more favourable habitats by the earlier breeding females, which limits site choice by those that come ashore later in the season. There are two lines of evidence for this. Firstly, female and neonate specialisation values tend to decrease throughout each season, which is indicative of niche widening over the season (a result of a wider range of EGVs being utilised). It may be that early in the season the niche is relatively narrow as females are able to choose their preferred sites within a restricted range of each EGV, but as choice of preferred sites becomes limited later in the season, a wider range of EGVs are encountered as less favoured sites become occupied. This supports the conjecture that the site choice of the earlier breeding females may determine the colonisation patterns and distribution of subsequent females (Anderson *et al.,* 1975). Secondly, the HS models based on data from early in each season generally perform better than those based on data from later in the same season. As the 'earlier' models perform better than the 'later' models, the global distribution of EGVs better predicts species presence in these models, suggesting that additional, unconsidered factors may be affecting the later models. These unconsidered factors include the possibility of conspecific interactions; these could arise as a consequence of preferential colonisation, with initial colonisers aggressively defending 'their' local resources (Soutullo *et al.,* 2006). This would decrease the resolution at which EGVs alone can predict HS as the relationship between EGVs and species presence breaks down in the presence of biotic interactions which force some individuals into typically less favourable sites. The overall increase in neonate specialisation at the end of 2009 and 2010 could be an unquantified effect of the weather conditions at the time but may also be related to the possibility of females leaving pups in less preferred areas and commuting between their preferred conditions and pups. If this were the case, the areas that pups are left in are unlikely to show a consistent change in conditions across seasons. Therefore, if pups are simply left in less preferred locations it is unlikely that any consistent trend in specialisation would become apparent through the widening or narrowing of neonate niches throughout the season.

In addition to these conspecific interactions, another factor that may influence female site choice is simply conspecific presence; female presence at a site will exclude that specific area from the options from which later-arriving females can choose to settle in. It is likely that a small area surrounding these sites will be also less favourable due to increased agonistic interactions

with ‘resident’ females (Soutullo *et al.,* 2006), from which they will maintain an average distance of 5.99m (±1.26m; SD) (Chapter 3). This is especially true for parous females, which are typically more aggressive towards conspecifics than those without pups (Bonner, 1981), presumably as a means of pup protection (Kovacs, 1987). As conspecific presence was not included in the ENFA, it is possible that increased conspecific presence may also have contributed to the generally poorer performance of HS models created using data from later in each season. The degree of female aggregation decreases over each season, suggesting that females would prefer to move further inland to unoccupied sites rather than occupy potentially more favourable sites near to settled females. This is in line with what may be expected from an IFD with unequal competitors, or the IDD (Fretwell and Lucas, 1970; Parker and Sutherland, 1986; Grand and Dill, 1999; Calsbeek and Sinervo, 2002), with females preferring to settle for sole occupation of potentially lower quality sites (much further from access) than share higher quality sites, especially given the increased conspecific aggression associated with high breeding densities (Stephenson *et al.,* 2007). The degree of competitive ability is likely to be affected by female age, size and by which individual is initially ‘resident’ at a site, though predicting the subsequent distribution of females is further complicated by the fact that individual females are unlikely to remain at a pool for the entire duration of her time on land and will have to commute between the pool and her pup, relinquishing control of the pool. However, any parallels with the IDD cannot be known for certain without a detailed assessment of the relative quality of occupied *versus* unoccupied sites. The incorporation of conspecific presence into SDMs is discussed further in Section 6.2.4.

Preferences for sites with intermediate proximity to pools and access are clear throughout the results of both Chapter 3 and the ENFA. However, the preferences for sites of low salinity have appeared somewhat more questionable given the preference for sites of higher than average salinity shown in 2009, and the seemingly inexplicable general trend for neonates to be found in sites of lower salinity than the females. However, as highlighted in Chapter 3, the difference between females and neonates may simply be an artefact of how the salinity surface was interpolated, and could thus be explained by female and neonate proximity to the nearest pool of water. Despite this, salinity was retained in the ENFA analyses. The apparent preference for sites of high salinity in 2009 simply shows that females and neonates were generally found at sites of higher salinity than is available *on average* over the SS. However, the average salinity for the SS is very low, and it appears that individuals typically avoid the higher salinity pools, as shown by the lower suitability of these pools indicated in all HS maps (e.g. Figure 4.8; this is also apparent in HS maps from 2009, JES *pers. obs.*). These pools are of such high salinity that it may be reasonably expected that one could discriminate between these and freshwater pools, though the difference between the global average salinity and the salinity at seal locations in 2009 is so minute that it is unlikely that seals have distinguished the difference and made a site choice on

this basis. This assumption was made on the basis of previous work by Friedl *et al.* (1990), who found that the gustatory threshold for salinity was 3.6‰ in California sea lions (*Zalophus californianus*). Importantly for this research, Friedl *et al.*'s work demonstrated that California sea lions can discriminate between salt (sea) water, which is typically approximately 35-36‰ salt (0.6M NaCl; Nicol, 1960) and fresher water, detecting the difference between fresh, distilled water and water of 3.6‰ salinity (0.1M NaCl; though perhaps even as low as 1.8‰, or 0.05M NaCl). Though there are likely to be interspecific differences between the California sea lion, an otariid, and the grey seal, this suggests that female grey seals are basing site choice partially on avoidance of high salinity areas. It is also possible that female grey seals face a trade off between sites of low CPOOL but high salinity and sites of high CPOOL but low salinity; given the importance of thermoregulation and proximity to their pup (Redman *et al.,* 2001; Twiss *et al.,* 2002), females might be expected to opt for sites with low CPOOL values and more moderate to higher salinities if faced with a choice; of course, this trade-off will also be affected by the number of females ashore and the availability of suitable sites. A further trade-off is found in the choice between high CACC-low salinity and low CACC-high salinity, and it may be that females would prefer to settle in areas of moderate salinity closer to access points to the sea than incur increased costs of locomotion to reach areas of very low salinity further up the slope to the south of the SS.

It therefore appears that females exhibit a preference for pools of lower salinity, avoiding high salinity pools throughout the SS. Assuming this is a real effect, it is unlikely that this is for any other reason than a taste preference exhibited by seals drinking from pools. This supports previous propositions that adult grey seals may drink from pools of water at North Rona (PPP and SDT, *pers. comm.,* Redman *et al.,* 2001), potentially to maintain a positive water balance (Redman *et al.,* 2001) and avoid the water stress brought on during lactation (Reilly *et al.,* 1996). To conclusively demonstrate salinity preferences we would ideally need to conduct experiments or make use of natural experiments in order to observe and quantify seals drinking to determine whether pools which seals drink from are of lower salinity than the average available.

Despite the drawbacks in mapping HS outlined above, the HS maps corroborate the results of Chapter 3 and the ENFA: the areas of highest suitability are consistently at intermediate distances from pools. The high suitability of areas near to pools is mediated by the proximity of a site to the nearest access, as those pools furthest from access show lower suitability than those at intermediate distances to access points. The same is true of salinity; areas around pools at intermediate distances to access are of lower suitability where salinity is high. It may therefore be concluded that proximity to pools is important to female site choice, but that the suitability of individual pools is determined by their proximity to access and salinity.

The range of HS values at sites occupied by females and neonates is consistent between all focal days, and the availability of high suitability areas appears to be consistent between years.

Furthermore, the availability of a range of habitat types, indicated by inter-annual consistency in EGVs, does not appear to change significantly between breeding seasons. This consistency in HS of each cell of the raster map of the SS is also indicated by the high degree of correlation in HS values between focal days within each season and within stages between each season. Despite this the North Rona colony has experienced a notable decline, as demonstrated by the reduction in number of females ashore each year between 1998 and 2010. As suggested in Chapter 3, it seems unlikely that the population decline is related to density-dependent effects of habitat availability. This is corroborated by the consistent range of HS values found at occupied sites between 1998 and 2010. Though Harwood and Prime (1978) suggested that the size of a colony could be restricted by the number of available pupping sites, the North Rona colony has previously supported a larger population within the bounds of the SS, so space should not be limiting. This raises the question of what could be causing the decline of the North Rona colony, especially since nearby colonies in the Outer Hebrides group are expanding (SCOS, 2011). Alternative drivers of the decline of the North Rona population are considered in Section 6.4.1.

Given the consistency observed in local HS between focal days and years, it is possible that the HS of an area could give rise to and/ or sustain the conservation of colonisation patterns between years. It has been suggested that the first females ashore influence the pupping sites of subsequent arrivals (Anderson *et al.,* 1975); the results presented here support this, and indicate that preferential colonisation of favourable areas by the first females ashore may occur on North Rona. These first females presumably select sites based on the EGV distribution and HS at each site encountered; inter-annual consistency in these values could cause these females to choose geographically similar sites each year, affecting the colonisation pattern as subsequent females come ashore and avoid already occupied sites and, possibly, contributing to the high site fidelity observed among the North Rona females (Pomeroy *et al.,* 1994). This raises the interesting prospect of site fidelity, in association with consistency in EGV and HS values between years, giving rise to individual 'knowledge' of sites and therefore an influence of past experience on future reproductive success. Previous observations of individual females being faithful to sites at which they previously reproduced unsuccessfully (PPP and SDT, *pers. comm.*) suggest that this may not be the case, though it would be interesting to investigate this in more detail.

ENFA has provided an easily interpretable method of analysing habitat and pupping site preferences of adult female grey seals, producing results that are in line with previous research at the North Rona colony. Importantly, limitations of the ENFA approach are few. As highlighted below, a more complex modelling approach is perhaps necessary to assess the impacts of changes in climatic conditions and conspecific presence on individual distribution, though in the elucidation of habitat preferences, ENFA has performed well. The common criticisms of PO SDM approaches (Zaniewski *et al.,* 2002; Phillips *et al.,* 2009) were considered whilst choosing an

appropriate modelling approach. For example, it is often stated that these methods suffer from a bias associated with a non-systematic, often *ad hoc* sampling regime (Zaniewksi *et al.,* 2002) which may suffer from a sample selection bias whereby some areas (generally the most accessible) in a landscape are more intensively sampled than others (Phillips *et al.,* 2009), or a sampling bias in rare *versus* common species (Ferrier and Watson, 1997; Zaniewski *et al.,* 2002). These 'drawbacks' are considered to be more applicable to PO than PA data (Elith *et al.,* 2011; Phillips *et al.,* 2009), but are not pertinent here. Firstly, only one species is being considered, whilst both age classes being examined are easily visible from the observation blind; this means that the criticism regarding the potential sampling bias associated with rare *versus* common species, is unsound in this case. Secondly, the method used for mapping seal distributions (Section 2.4.2) was thorough and systematic, with equal sampling effort applied over the SS, leaving very little chance of individuals being overlooked or incorrectly mapped.

Though the mean of the species distribution differs somewhat from that of the global distribution, the specialisation factor for each focal day indicates that the grey seal is relatively widespread relative to the available EGVs; this further supports the use of a PO modelling approach which does not incorporate pseudo-absences generated from background areas. Incorporating pseudo-absences is likely to result in biased absence data where the species is widespread, or where presence data is scarce (Boyce *et al.,* 2002), as is occasionally the case in the early stages of each breeding season. Another criticism of PO approaches such as ENFA is that the lack of absence data precludes the inclusion of biotic interactions such as competition and exclusion in models (Guisan and Zimmerman, 2000), which would otherwise be represented by absence of the focal species from an area. However, in this case ENFA, as a PO method, provides an ideal approach to modelling grey seal site preferences. This is because the breeding phase of the grey seal life cycle is entirely independent of the constraints on habitat selection of foraging requirements and, at least at North Rona, is independent of *hetero*specific competition for space and resources. It is, therefore, clear that the use of absence data to take these interactions into account would be unnecessary. Despite the lack of competition with heterospecifics, it may be that conspecific interactions *do* limit site choice either simply through preferential colonisation of favoured sites by the first females ashore or through the effects of aggressive interactions which limit the density at which individuals can occupy more favourable areas, as suggested above.

It is possible to incorporate such interactions into a PO framework. In Chapter 5, the presence of adult females is included in a 'cost-distance' to female surface to assess how this influences the distribution of neonates and weaners. However, the same surface could not be applied in the female ENFA: as each female presence would be included in the cost-surface, each female location in the ENFA presence input data would have a 'cost-distance' to nearest female value of 0 (itself). A surface depicting 'cost-distance' to next-nearest female represents an

alternative approach; however, this would be very similar to a density map, so the ENFA would predict seal distribution using a 'pseudo-density' EGV, which would be rather circular, predicting high suitability in areas of high seal density largely due to the density, rather than abiotic conditions. Despite these difficulties, this seems like a promising avenue for further research, since the presence of an individual at a site renders that site unusable by subsequent arrivals and may also limit the suitability of nearby site due to the occurrence of costly aggressive interactions (Soutullo *et al.,* 2006; Stephenson *et al.,* 2007). It is possible that a more complex iterative modelling procedure could be performed which accounts for female presence, incorporating individual presences and behavioural metrics into cost-surfaces such that the presence of conspecifics also acts as a barrier to movement, and a field of influence around each adult individual could be used to represent higher cost of aggressive interactions in that area. Such an approach would assess the habitat and pupping site choice of each female as she arrived on the colony, taking into account the restricted availability of sites resulting from conspecific presence. Such an individual-based model of colonisation would avoid the circularity identified above relating to the CFEM EGV and provide a more precise interpretation of female choices. This is important as a deeper understanding of the intra-seasonal change in habitat preferences would require that the changing availability of suitable habitat be taken into account (Arthur *et al.,* 1996). As outlined above, this would require a more complex, iterative approach to model the surface and assess HS. Agent-Based Modelling could prove fruitful in this respect (Kanarek *et al.,* 2008; McLane *et al.,* 2011; Semeniuk *et al.,* 2011), though was beyond the scope of this research.

The possibility of SDMs being affected by unquantified inter-individual interactions is a subject that has received increased attention in recent years, with a number of solutions being proposed (e.g. Durães *et al.,* 2007; Fischhoff *et al.,* 2007; Pérot and Villard, 2009; Semeniuk *et al.* 2011). In this case, individual interactions may have lead to the deterioration in HS model quality over each breeding season indicated by the CBI scores. With this in mind, it may be more productive to consider only the HS models and ENFA results produced using data from the beginning and early stages of each season to be indicative of real site choice, as these are the stages of the season likely to be influenced the least by prior colonisers. The beginning stage of the 2010 season represents the earliest available date on which the ENFA analysis was performed and demonstrates that females show clear preferences for proximity to low salinity pools at intermediate distances to access points. It would be beneficial, therefore, to perform an ENFA on EGV and seal distribution data from earlier in each season. However, the limited availability of aerial photographs from the beginning of each season restricts this progression.

The above discussion highlights a difficulty that faces all niche modelling techniques: many variables are unmeasureable or unknown, and their absence from models may introduce an unquantifiable bias (Hirzel *et al.,* 2001; McPherson and Jetz, 2007). These factors may be

ecological, including factors such as inter- or intraspecific competition (as is the case with the potential conspecific competition amongst breeding grey seals), or may be related to historical colonisation patterns, or disease events that have eradicated a species from an area. Finally they may be spatial effects, including barriers to movement such as those considered and incorporated here, or corridors that ease movement between areas whilst avoiding those in between (Hirzel *et al.,* 2001). It has previously been noted (Guisan and Zimmerman, 2000; Hirzel *et al.,* 2001) that SDMs therefore only represent a snapshot of the situation under consideration and, therefore, lack generality, which is sacrificed for reality, precision and applicability to the 'true' species niche. However, this does not preclude the use of such techniques in assessing EGV preferences and their change over time, as performed here; rather, these techniques provide an essential level of understanding of ecological preferences given several caveats regarding data quality and quantity.

In considering the generality of the ENFA results it is important to bear in mind that ENFA determines preferences of a species based on its locations *relative* to the EGVs within a defined study area. Marginality and specialisation are thus highly dependent on the size and extent of the chosen study area. This does not have severe implications for the comparisons made in this research due to the strictly defined nature of the SS, the extent of which covers all observable land accessible to the seals. However, most species generally respond differently to the varying combinations of environmental variables in different parts of their range (Boyce and McDonald, 1999; Mysterud and Ims, 1999; Osborne and Suarez-Seoane, 2002; Whittingham *et al.,* 2007), which has implications for the transferability of ENFA model outcomes to other areas (Fielding and Haworth, 1995; Randin *et al.,* 2006). In essence this means that the conclusions drawn here cannot easily be extrapolated to other colonies, which often have distinct topographies. Indeed, at some major breeding colonies, such as Donna Nook, pools rarely form and access is more open than at North Rona, which places the pupping site and habitat selection of females in an almost entirely different spatial and topographical context. These topographical differences have dramatic implications for the behavioural context of the site, likely including the level of male harassment (Boness and James, 1979; Lidgard *et al.,* 2001), which may also influence female site choice. As this approach has assessed the realisation of the species niche within a strictly defined site, it would be interesting to assess female site preferences at topographically distinct colonies, at which the importance of these EGVs may be altered, or masked by other EGVs or social factors not considered here. Further potentially influential covariates, and the possible effect of a lack of pools of water are considered in further detail in Section 6.3.1.

ENFA and subsequent HS mapping are insensitive to the number of presence points or the input order of EGVs (Hirzel *et al.,* 2001; Sattler *et al.,* 2007). Therefore, when ecological interpretation of the output is a key aim, ENFA is likely more useful even in situations where alternative models (such as GLMs, which are sensitive to these aspects of the data) might provide

a higher correlation to observed data (Hirzel *et al.,* 2001). ENFA therefore provides excellent support to the researcher interested in determining basic ecological preferences of a focal species, overcoming some of the drawbacks generally highlighted for PO techniques. Furthermore, ENFA and the more established measurements of niche overlap integrated into BioMapper clearly provide an excellent resource for determining and differentiating the requirements of different species or conspecific age classes. This is especially true of research in which the ecologist has a reasonably sound understanding of the factors likely to influence species distribution; in other cases it may be that the performance and predictive ability of SDM approaches such as ENFA could suffer from the inclusion of poorly selected and superfluous EGVs. Conversely, the correlation trees and covariance matrix produced in BioMapper when computing an ENFA ensure that the researcher is provided with a solid basis for EGV inclusion or removal; EGVs may then be selected based on sound ecological knowledge, rather via model selection. Many studies utilise this somewhat arbitrary model selection technique, having included a wide variety of potential predictors simply because they are readily available and *might* influence the species' distribution (Elith and Leathwick, 2009). There is a strong argument for, instead, including only those EGVs that are ecologically relevant to the focal species, building upon existing knowledge and theory and avoiding the "statistical tinkering" of model selection (MacNally, 2000:668). Moreover, the ENFA process of creating composite factors from input EGVs ensures that only those EGVs that explain a significant amount of the variance influence the model. An additional advantage of ENFA over other techniques, including PCA, is that the factors produced are easily interpretable in terms of the input EGVs (see Section 4.1.2). Previous studies have shown that interpretation of the factors in this way corroborates the experience of field experts who may have identified qualitative links between EGVs and species distribution (Hirzel *et al.,* 2002). This is certainly true in this case, as the marginality factor for each focal day substantiates previous observations (e.g. Pomeroy *et al.,* 1994; Redman *et al.,* 2001; Twiss *et al.,* 2000a; 2001).

Despite the generally good performance of BioMapper in this study, caution is advised in drawing conclusions from the HS maps produced for widespread, generalist species (those with broad ecological niches), for which HS maps are generally more difficult to predict than for marginal species (Stockwell and Peterson, 2002; Seoane *et al.,* 2006; Sattler *et al.,* 2007). Furthermore, it may be that an alternative assessment of HS model performance should be sought as those methods provided in BioMapper appear to be sensitive to the marginality of the species in that more widespread species, whose ecological requirements are closely matched by the EGVs available over the SS, produce models that are subsequently assessed as being little different from random. Finally, the jack-knife cross-validation method may be more useful when data quantity is high, as a greater number of presence points would allow more partitions to be confidently used. In other cases bootstrapping (sampling with replacement) may be more useful,

despite the potential risk of this approach being overly optimistic in its assessment of model performance (Fielding and Bell, 1997; Hirzel and Guisan, 2002). The main flaw with BioMapper is therefore that it provides no bootsrapping-based validation methods. An alternative approach is of course to evaluate the models with independent data sets; however given the temporally and spatially variable nature of the EGVs utilised, independent data from other days is likely to provide an inaccurate assessment of model performance. A related drawback is that BioMapper does not include confidence intervals on the HS maps (Hirzel *et al.,* 2002). However this is more important in studies aiming to inform decisions in conservation and management programmes, whilst studies undertaken to describe habitat preferences have less immediate need for such accuracy. This study is based predominantly on the ENFA results, with a focus on understanding the EGV preferences of female grey seals, and how these changes within and between seasons. The HS values derived subsequently are merely used as broad descriptions of the SS.

Though the means of validation of HS model performance is clearly important, more important is the method used in model creation. For this research, the Distance Geometric Mean algorithm was used to build the HS maps as it seemed to be the most appropriate technique of those available (Section 4.2.3). However, the use of density-based metrics of HS have been questioned (Mosser *et al.,* 2009), as they implicitly assume an ideal free distribution of individuals (Fretwell and Lucas, 1970). This is a problem common to all distribution and niche models that assess HS based on the distribution of individuals, rather than being specific to ENFA. In the present case, the possibility of preferential colonisation and consequent competitive exclusion brings the validity of the IFD assumption into question. As discussed in Section 6.2.2, an alternative method incorporating demographic and/or reproductive parameters may be more informative in assessing the HS of particular EGV combinations at available sites, as achieved by Titeux *et al.* (2007); this could represent an important step forward in understanding the influence of the physical environment on HS.

In conclusion, ENFA provided an appropriate and useful technique to assess the habitat and pupping site preferences of female grey seals based on ecologically relevant variables, confirming the results of previous studies in establishing preferences for proximity to pools at intermediate distances to the limited access points available at North Rona, likely in response to a need for behavioural thermoregulation. It also provided support to previous observations that seals also use the pools to maintain a positive water balance during lactation, rather than simply for thermoregulation. Areas of high and low suitability match those expected based on expert knowledge of the distribution of prime habitat conditions at North Rona. The change in preferences over each breeding season suggests preferential colonisation of prime sites early in the season, with subsequent site choice mediated by conspecific presence, and probably aggressive interactions amongst unequal competitors.

5. Ontogenetic Changes and Biotic Influences on Pup Distribution

5.1 Introduction

Intraspecific competition and niche segregation has been increasingly recognised as a driver of conspecific differentiation in resource use, operating alongside the long-studied interspecific competition that has been the focus of many studies into resource utilisation, niche segregation, and divergent evolution (e.g. MacArthur and Levins, 1967; Ashmole, 1968; Richards *et al.,* 2000; Tilman, 2004; Donadio and Buskirk, 2006; Grant and Grant, 2006). When considering intraspecific segregation, researchers have often focused on inter-sexual resource and habitat segregation, particularly amongst sexually dimorphic species (Mysterud, 2000) such as the red deer (*Cervus elaphus*; e.g. Conradt *et al.,* 2001) or the Galápagos sea lion (*Zalophus wollebaeki*; Wolf *et al.,* 2005). However, another important component of intraspecific niche segregation is the segregation of resource use between age classes (Polis, 1984), which may arise as a direct result of differences in body size (e.g. Hobbs and Munday, 2004; Davey *et al.,* 2005), nutritional requirements (e.g. Fishelson *et al.,* 1987; Cooper *et al.,* 2007) or food handling capabilities (e.g. Werner and Gilliam, 1984; Herrel and Gibb, 2006), or simply through exclusion of young individuals from territory held by dominant older individuals (e.g. Strickland, 1991; Hogstad, 2008). Whilst a lot of research into intraspecific competition and niche segregation has focused on food resource availability and segregation, the advent of spatial tracking and analysis technologies has allowed more recent research into the effects of competition on fine-scale site use, relating to two- or three-dimensional geographic space rather than food or shelter selection (e.g. Anderson *et al.,* 2002). This allows the influence of conspecific presence to be directly incorporated into models to establish biotic effects on space use (e.g. Stephenson *et al.,* 2007; Knip *et al.,* 2011). In the grey seal, behaviour on the breeding colony is independent of foraging requirements and space use is, therefore, unaffected by foraging ability; however, it remains plausible that younger individuals may be excluded from favoured areas by older individuals which show a preference for sites close to pools of low salinity at intermediate distances to access (Chapter 4). In this chapter, the possibility of exclusion of weaners (Stage V pups) from particular areas by adult individuals will be assessed by examining their locations on the colony relative to the locations of neonates (Stage I-II pups). This is important due to the extended periods of time for which different grey seal age classes must co-exist on-land during the breeding season, as detailed below, and the likely effect of topography and the environment on pup mortality (Twiss *et al.,* 2003).

During lactation, grey seal pups gain an average of 1.7kg day^{-1}, typically up to a weight of approximately 40kg at Stage V (Pomeroy *et al.,* 1999). Mothers then abruptly wean their pup, generally on the 18^{th} day post-partum, before mating and returning to the sea. After weaning, weaners stay on the colony for up to several weeks before entering the sea (Bonner *et al.,* 1981;

Bennett *et al.,* 2007). During this time they undergo a post-weaning fast (PWF), dramatically reducing their metabolic rate and drawing on their blubber reserves to meet their daily energy requirements until they acquire their first solid meal at sea (Coulson and Hickling, 1964; Nordøy and Blix, 1985; Worthy and Lavigne, 1987; Nordøy *et al.,* 1990). This metabolic depression occurs very rapidly, with a 45% reduction in just 10 days after weaning (Nordøy *et al.* 1990). The terrestrial PWF is a phase that presents an evolutionary dilemma in terms of female resource allocation. Given the implications of maternal body condition for adult female survival, it might be expected that females would be more conservative in their investment in pups, transferring an 'optimum' amount of energy to their pup each year, without transferring a surplus that could sustain a substantial PWF. Despite this, pups undergo a considerable PWF of variable duration, suggesting that pups that receive adequate provisions to sustain a substantial PWF may accrue some sort of benefit in this time that offsets the presumed loss of fitness that occurs through consumption of critical energy reserves.

Whether the terrestrial PWF has a specific function is unclear, though various studies have shed some light on the factors affecting this phase. It appears that the duration of the PWF is partly determined by the topography of the colony, particularly the ease of access. Where access to and from the colony is possible in sheltered waters, pups may become accustomed to the water prior to weaning and, therefore, tend to leave the colony earlier. At North Rona, the shore is rocky, lacking the beaches common at many colonies, and is bordered by rough sea conditions which preclude this and the stay on land is, therefore, relatively longer (Hewer, 1974). Other possible explanations for the existence of the PWF include a 'reluctance' or inability of the weaners to move through areas of high adult density towards the sea or may aid in the 'learning' of the natal site, possibly facilitating natal philopatry in a fashion similar to the 'Natal Habitat Preference Induction' phenomenon, whereby experience of the natal site shapes future habitat preferences (Davis and Stamps, 2004). Also, a simple reduction in thickness of the blubber layer to reduce buoyancy combined with a period of muscular development may enable more efficient diving on foraging trips (Butler, 2000; Sparling and Fedak, 2004; Bennett *et al.,* 2010), though this is likely to be a complex relationship, since heavier southern elephant seal pups have been found to dive deeper and longer than lighter pups (Hindell *et al.,* 1999) and body composition (i.e. the proportions of muscle and fat) may, therefore, be important. However, these alternative explanations do not address the evolutionary dilemma in maternal resource allocation described above. If females provisioned their pups less on average then the PWF would not be required for the utilisation of 'excess' lipid stores. However, a large amount of empirical evidence suggests that the PWF allows pups to develop an appropriate diving physiology. This argument has received considerable support from Noren *et al.* (2005), who found that the mass-specific oxygen stores of pups increase by 35% over the PWF, through increases in levels of haemoglobin,

haematocrit and myoglobin, in addition to increases in blood volume. Pups are weaned in a range of body conditions, differing by as much as 50% (Pomeroy *et al.,* 1999) and there is a large amount of plasticity in the duration of the PWF. It has been suggested that this plasticity allows weaned pups of variable conditions and body compositions to depart for the sea with sufficient energy reserves for foraging (Noren *et al.,* 2008). Generally, pups that are larger at weaning spend longer ashore than smaller pups, possibly further enhancing dive capabilities through development of oxygen stores (Bennett *et al.,* 2010). It may be that smaller pups face a greater dilemma in terms of the trade-off between departure mass and dive capabilities, and leave the colony sooner after weaning than larger pups, before their energy reserves become too depleted but before their dive capabilities have developed as fully (Bennett *et al.,* 2010). It is also important to recognise, however, that body condition only explains a small amount of variation in PWF duration, leaving approximately 86% of the variability unexplained (Noren *et al.,* 2008). It has been suggested that the remaining variance may be explained by a combination of factors including topography and individual differences in development and energy metabolism.

During the PWF it is clear that energy conservation is important, as indicated by the rapid decrease in metabolic rate observed (Nordøy and Blix 1985; Nordøy *et al.* 1990). Furthermore, it is likely that energy conservation mechanisms may extend to pup behaviour, with limits to movement and other costly activities such as involvement in aggressive interactions, especially given the extended duration of the fast. However, there have been no studies of the movements or behaviour of weaned grey seal pups, with current knowledge restricted to qualitative behavioural observations and data on metabolic changes. Previous studies have noted that weaned pups often move towards higher ground, away from the main colony (e.g. Coulson and Hickling, 1964). These purely qualitative observations have been supported by subsequent observations which suggest a degree of avoidance of interactions with adults (e.g. Hewer, 1974, Twiss *et al.,* 2001). More recent studies have investigated the habitat choices of adults and the selection of pupping sites (Pomeroy *et al.,* 2000a; Twiss *et al.,* 2000a, 2001, 2003; Chapter 4), but none have explicitly assessed the 'choices' of weaners. The data available here (Section 5.2.1) provide an opportunity to investigate this and delineate the preferences of weaners relative to the pupping site choices of adult females, which may also address the possibility of interactions between adults and weaners. Hirzel and Le Lay (2008) highlight that relatively few SDM studies address niche interactions or compare the niches of multiple species, but note that this can be fruitful in allowing inference regarding interactions such as competition and spatial segregation; the same is true of such studies focussing on different conspecific age groups. Classical measures of niche overlap (e.g. Colwell and Futuyama, 1971; Hurlbert, 1978) have rarely been utilised alongside SDM in order to achieve this, though a combination of these is useful in assessing or predicting such interactions (e.g. Sattler *et al.,* 2007). A similar approach will be applied here; in

addition to assessing the degree of separation in resource use between older (Stage V, 'weaner') and younger (Stage I-II, 'neonate') pups regarding the EGVs CACC, CPOOL and salinity, this chapter will also quantitatively assess the difference in neonate and weaner distance to nearest adult female, as previous studies (e.g. Twiss *et al.,* 2001) have suggested that this may be important in determining weaner distribution due to adult aggression towards non-filial and weaned pups.

5.2 Methods

Following initial exploratory analyses of pup distributions (Section 5.3.1), the degree of niche overlap between neonates and weaners was assessed and discriminant analysis was then performed in BioMapper to discriminate the niches of neonates and weaners (Section 5.3.2), as described below. The data implemented in these analyses relates solely to the 2010 breeding season. Due to the timing of pupping and the subsequent temporal distribution of weaners, it was only possible to analyse the two latest focal dates using discriminant analysis (Late and End 2010). 2010 was chosen as it is one of the seasons with the most complete data sets, as the salinity surfaces used are specific to that year, rather than being averages as in 1998, 2004 and 2008. Also, though there is some inter-annual variation in resource (CPOOL and salinity) distribution (Section 3.3.1), 2010 was deemed to adequately represent the conditions during other seasons.

5.2.1 Input data

The data described below were processed for use in BioMapper as outlined in Section 3.2.

5.2.1.1 Presence data

The pup presence data were collected by PPP as described in Sections 2.4.1 and 2.4.2. This gave a total of 79 presences for late 2010 (58 neonates and 21 weaners) and 110 presences for the end of 2010 (41 neonates and 69 weaners). For exploratory analyses considering all dates of the 2010 breeding season, a total of 2825 locations were analysed (2179 neonates and 646 weaners). Weaner and neonate location coverages were converted to grids of 0.2m × 0.2m resolution. To create a Boolean grid map of seal presences at the same resolution as the EGV maps, as required for BioMapper analyses, these grids were then aggregated to a coarser 1m × 1m grid cell size, with each cell conveying the presence or absence of seals in that area. Pup location data were also analysed for degree of clustering on each day in 2010; this approach is described in detail in Section 3.2.3, with supplementary information in Appendix 1.

5.2.1.2 Ecogeographical variable data

The SS, as defined in Section 2.3, was characterised using the four EGVs elevation, CACC, CPOOL and salinity at a 1m × 1m grid cell resolution. Based on results from Chapter 4 (see Section 4.2.1.3), the EGV ELEV was excluded from further analyses. The collection and manipulation of the EGV data is described in detail in Section 2.4. CACC remained constant over the breeding season

and between years, as this describes permanent features of the island of North Rona itself, and so was computed only once. On the other hand, CPOOL and salinity were variable within the 2010 season, so a new grid was created for each focal date, as described previously (Section 2.4). In addition to these three EGVs, a surface was created which represented the 'cost-distance' to nearest female (CFEM) for each location in the SS for each focal date. The CFEM surface was created using the ArcInfo command PATHDISTANCE, as described for CACC and CPOOL (Sections 2.4.4.1 and 2.4.4.2). GIS coverages containing data on female locations for each focal date were converted to 0.2m × 0.2m grids which were used as input grids for this process.

5.2.2 Neonate and weaner niches: Breadth, overlap and discriminant analysis

'Niche' breadth was analysed using Hurlbert's Niche Breadth Index (*B'*; Hurlbert, 1978) which was calculated for each EGV in turn, essentially describing the breadth of resource use for neonates and weaners. Comparisons of competing breadth and overlap measurements, including *B'*, have generally concluded that those most commonly used produce similar results, and that none may be considered superior to the others (Krebs, 1999; Zabala *et al.,* 2009). *B'* was chosen as it is in widespread use and takes into account the relative availability of resources, meaning that the use of globally rare resources is given greater weight than common resources (Hurlbert, 1978); this seems appropriate given the fine scale at which the topography varies on North Rona. 'Niche' overlap between neonates and weaners was analysed using Pianka's Overlap Index. This index was chosen as it is in widespread use and is useful in that its values range from 0 to 1, making interpretation simple. Discriminant analysis (DA) was then performed in order to discriminate between the two niches for each focal date. DA utilises the same input as ENFA but, unlike ENFA, computes a single discriminant factor using both 'species' presence maps at the same time. This factor is computed on the combination of EGVs which best 'separates' the two niches, i.e. those EGVs on which site usage most differs (see Section 4.2.4 for more detail).

5.3 Results

5.3.1 Pup distribution

Neonates were present on the colony from the first day of the 2010 breeding season (28th September, the first day of mapping); however, weaners were not prevalent on the colony until later in the season. The first was observed on 13th October (Figure 5.1). During the period of observation (up to 3rd November, inclusive), the most weaners seen on North Rona at any one time was 70 (3rd November). To describe the pattern of pup dispersion, the observed daily mean distance between nearest pup neighbours (within each 'age group', i.e neonate distance to nearest neonate and weaner distance to nearest weaner) was compared with the expected daily mean distance for both a random arrangement and a maximally dispersed arrangement of points (see Section 3.2.3 for details). This approach indicated more clustering in both neonate and

weaner locations than would be expected by chance on all dates (Appendix 4, Tables A4.1 and A4.2). In addition, the nearest neighbour index '*R*' was calculated for each day, using neonate and weaner locations separately. This indicated clustering on all dates for both neonates and weaners but also indicated that they became less clustered as the season progressed (Appendix 4, Tables A4.3 and A4.4), as shown in Figure 5.2. Comparison with tables of critical values in Appendix 1 (Tables A1.1 and A1.2) indicated that the results for *R* were significant at $\alpha = 0.001$. Furthermore, *R* was significantly positively correlated with day of breeding season (Figure 5.2; Pearson's Product-Moment Correlation; neonates: r = 0.899, $p < 0.001$; weaners: r = 0.511, $p = 0.018$).

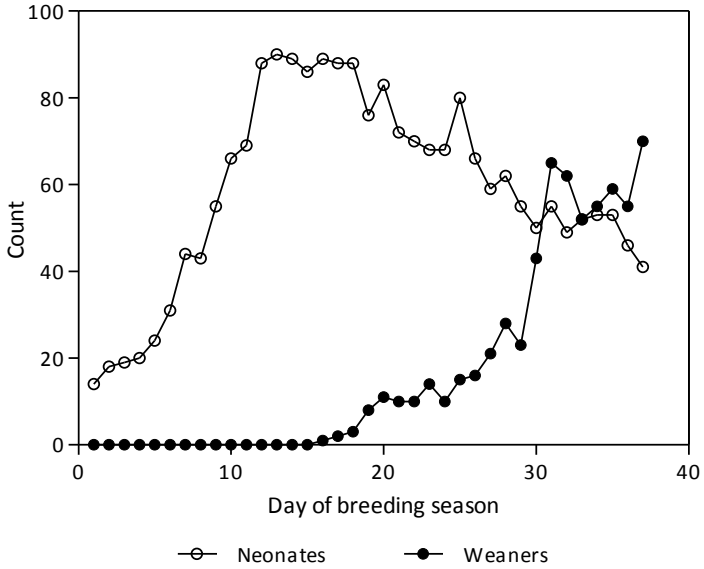

Figure 5.1: Count of neonates and weaners observed on each day during the 2010 breeding season. First Stage V pup sighting = 1 pup on 13th October. Day 1 = 28th September.

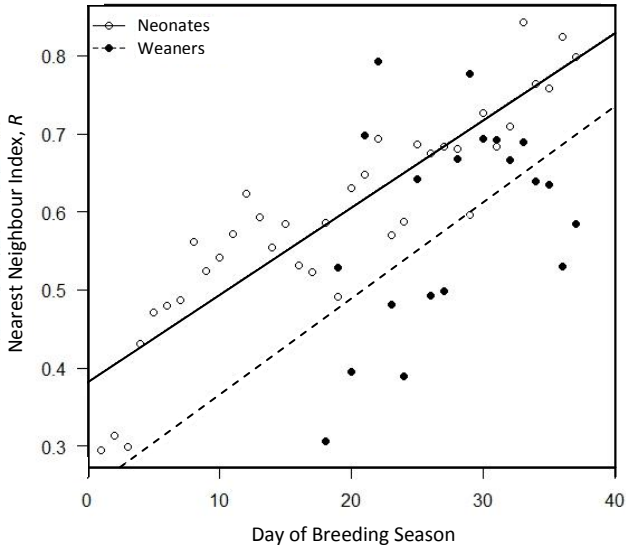

Figure 5.2: Change in nearest neighbour index (*R*) over 2010. Day 1 = 28th September. Positive correlation significant in both cases (Pearson's product moment correlation; neonates: r = 0.899, $p < 0.001$; weaners: r = 0.511, $p = 0.018$).

As shown in Figure 5.3, weaners were significantly further from the nearest adult female than neonates on both focal dates (Mann-Whitney U; Late 2010: U = 245.0, $n_{neonates}$= 59, $n_{weaners}$= 21; $p < 0.001$; End 2010: U = 66.0, $n_{neonates}$= 41, $n_{weaners}$= 70; $p < 0.001$). The same is true across all

dates of the 2010 season (Figure 5.2; Mann-Whitney U; U = 108531.5, $n_{neonates}$= 2179, $n_{weaners}$= 633; $p < 0.001$). In addition to being further from females than neonates, weaners get increasingly further on average from females as the season progresses (Pearson's product-moment correlation, df = 20; r = 0.552, p = 0.008; performed on data $\log_{10}$ transformed for normality), though neonates typically stay the same distance from females throughout the season, as shown in Figure 5.4. Though daily average neonate distance to nearest female declines across the season (Figure 5.4), the effect size is very small (Pearson's product-moment correlation, df = 20; r = - 0.057, $p < 0.001$; performed on data $\log_{10}$ transformed for normality).

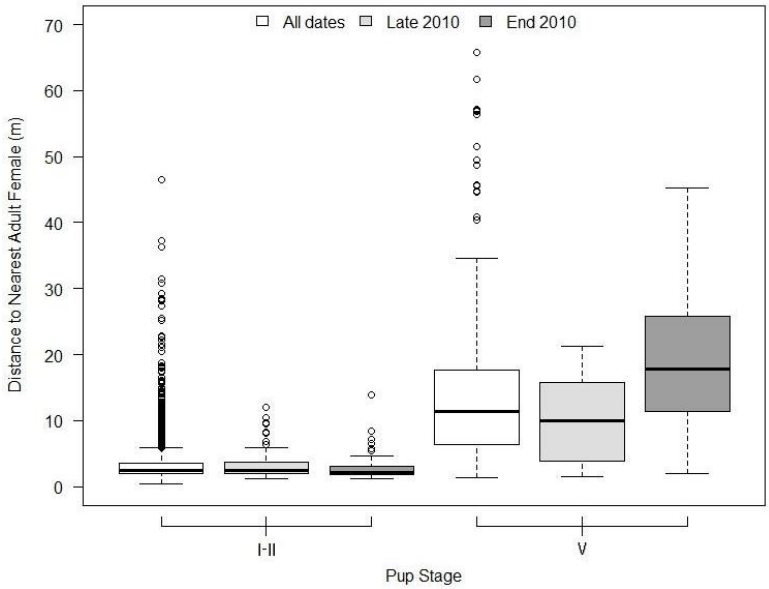

Figure 5.3: Difference between Stage I-II and Stage V pups' distance to nearest adult female for all dates during 2010, highlighting the pup-female distances on focal dates (Late and End 2010).

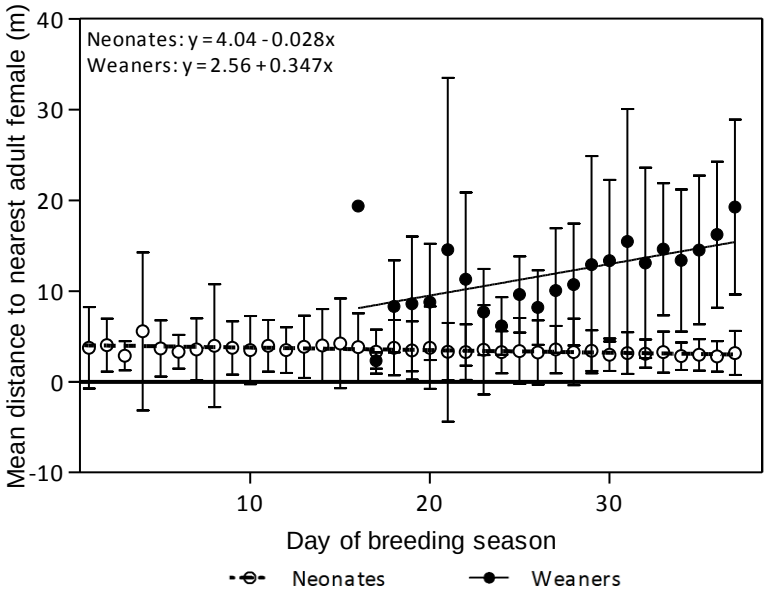

Figure 5.4: Daily average distance to nearest adult female for all neonates and weaners on the colony during 2010. Day 1 = 28th September. Regression lines of best fit indicate an increase in distance between weaners and their nearest female as the season progresses, whilst neonates maintain a relatively constant distance to their nearest adult female throughout the season Error bars demonstrate ± 1 standard deviation.

5.3.2 Discriminating the niches of neonates and weaners

The same CACC and salinity surfaces were used for both late and end 2010 (Section 2.4.4); however, the global distribution of CPOOL and CFEM both change significantly between late and end 2010 (Table 5.1): the SS becomes wetter on average (mean CPOOL decreases), whilst CFEM increases as the average distance to nearest female increases between the breeding season stages (Figure 5.5; Table 5.2). MULTCOMP analysis of the mean EGV values at locations of neonates indicates that they do not alter their distribution relative to any of the four EGVs between late and end 2010, though weaners are found closer to pools and in areas of higher salinity at the end of the season that late in the season (Figure 5.5; Table 5.1). Weaners are also found significantly further from adult females at the end of the season than late in the season (Figure 5.5; Table 5.1) and are always found further from adult females than are neonates. During the late stage of 2010, the mean CACC values of neonate and weaner locations did not differ significantly from each other or from the global distribution (Figure 5.5; Table 5.3). At the end of 2010, neonates are found at a higher CACC than is available on average over the SS, and than is occupied by weaners, whose average does not differ significantly from that for the SS as a whole (Figure 5.5; Table 5.3). Neonates are found significantly closer to pools than weaners are during late 2010, but are equidistant from pools at the end of 2010 (Table 5.3). However, during the end stage of 2010, neonates are found in locations with a mean CPOOL value that does not differ significantly from that available over the SS, whilst weaners are found closer to pools, at significantly lower CPOOL values than are available over the SS on average (Figure 5.5; Table 5.3). Weaners are found at sites of significantly lower mean salinity than either neonates or the global mean during late 2010, whilst neonates are found at sites with a mean salinity that does not differ from the global mean. At the end of 2010, neonates are found at sites with a mean salinity that is significantly higher than the SS average (Figure 5.5; Table 5.3), though they do not differ significantly from the mean salinity at weaner locations.

Table 5.1: Results of MULTCOMP tests for differences in mean species and global EGV values between stages of the 2010 breeding season. P-values for significant differences highlighted in bold. CACC: 'Cost-distance' to access; CPOOL: 'Cost-distance to nearest pool'; CFEM: 'Cost-distance' to nearest female.

Pup Stage	Comparison	t-value	*p*
Neonate	**CACC Late – CACC End**	1.473	0.144
	CPOOL Late – CPOOL End	0.720	0.473
	Salinity Late – Salinity End	-1.509	0.135
	CFEM Late – CFEM End	-0.805	0.423
Weaner	**CACC Late – CACC End**	-0.929	0.355
	CPOOL Late – CPOOL End	-2.628	**0.010**
	Salinity Late – Salinity End	2.081	**0.040**
	CFEM Late – CFEM End	4.887	**<0.001**
Global	**CACC Late – CACC End**	0	1
	CPOOL Late – CPOOL End	-95.6	**<0.001**
	Salinity Late – Salinity End	0	1
	CFEM Late – CFEM End	13.07	**<0.001**

Table 5.2: Summary statistics for EGV distributions and mother-pup distance (MPdis) for both neonates and weaners and the global EGV distribution during late and end 2010. Means and SD are presented rather than medians and IQR as MULTCOMP assesses differences in means (for more details see Section 3.2.2).

EGV	Period	Neonates		Weaners		Global	
		Mean	SD	Mean	SD	Mean	SD
Cost-distance to nearest access	**Late**	28.76	14.66	28.17	11.50	31.64	22.36
	End	32.83	12.41	25.25	15.02	31.64	22.36
Cost-distance to nearest female	**Late**	3.80	2.92	10.56	7.38	26.98	22.41
	End	3.35	2.48	20.57	10.00	28.48	23.85
Cost-distance to nearest pool	**Late**	7.78	7.64	13.18	8.78	16.27	13.32
	End	8.88	7.22	7.49	7.51	10.71	10.03
Salinity	**Late**	0.80	0.51	0.35	0.45	0.83	1.37
	End	1.22	0.66	0.70	1.10	0.83	1.37
MPdis	**Late**	3.55	2.64	10.05	6.87	-	-
	End	3.16	2.42	19.51	9.47	-	-

Table 5.3: Results of MULTCOMP tests for differences in mean EGV values between pup stages and between pup stages and the global EGV distribution for late and end 2010. P-values for significant differences highlighted in bold. CACC: 'Cost-distance' to access; CPOOL: 'Cost-distance to nearest pool'; CFEM: 'Cost-distance' to nearest female.

Stage of Season	EGV	Comparison	t-value	*p*
Late	**CACC**	**P2 – P5**	-0.182	0.981
		P2 - Global	1.481	0.286
		P5 - Global	1.346	0.354
	CPOOL	**P2 – P5**	2.447	**0.034**
		P2 - Global	8.381	**<0.001**
		P5 - Global	1.571	0.242
	Salinity	**P2 – P5**	-2.371	**0.043**
		P2 - Global	0.199	0.977
		P5 - Global	4.836	**<0.001**
	CFEM	**P2 – P5**	3.993	**<0.001**
		P2 - Global	58.766	**<0.001**
		P5 - Global	9.941	**<0.001**
End	**CACC**	**P2 – P5**	-2.831	**0.012**
		P2 - Global	-0.605	0.809
		P5 - Global	3.506	**0.001**
	CPOOL	**P2 – P5**	-0.946	0.597
		P2 - Global	1.604	0.231
		P5 - Global	3.526	**0.001**
	Salinity	**P2 – P5**	1.102	0.497
		P2 - Global	3.069	**0.006**
		P5 - Global	1.019	0.549
	CFEM	**P2 – P5**	13.509	**<0.001**
		P2 - Global	62.604	**<0.001**
		P5 - Global	6.506	**<0.001**

A degree of resource use (referred to here as 'niche') overlap between neonates and weaners is clear on all EGVs for both the late and end stages of 2010 (Figure 5.5). This is confirmed through the use of Pianka's Niche Overlap Index, *O* (Table 5.4). Despite this high degree of overlap, discriminant analysis was used within BioMapper in an attempt to assess niche differentiation between the age groups, with a primary focus on pup in space use relative to the distribution of females. Pianka's overlap index indicated that this was the EGV on which the niches of the neonates and weaners overlapped least (Table 5.4), especially later in the season, as indicated by direct comparison of the distributions displayed in Figure 5.5. This is potentially informative in itself, as the niches (CFEM resource use) overlapped substantially more in the late

stage of the season than at the end, suggesting active movement of weaners to areas further from females as the season progressed relative to neonates. As highlighted in Section 4.2.4, in order to perform DA effectively, the 'positive' and 'negative' age classes (as defined by their distribution on the discriminant factor) should be clearly distinguishable. In both cases, weaners were distinguishable as the 'negative age class' (Figure 5.6). On both focal days, discriminant analysis indicated that weaners are typically 'favoured' by sites further from adult females but closer to access points and of higher salinity than neonates (Table 5.5). In late 2010 weaners are found further from pools than neonates, however this is reversed at the end of 2010 (Table 5.5).

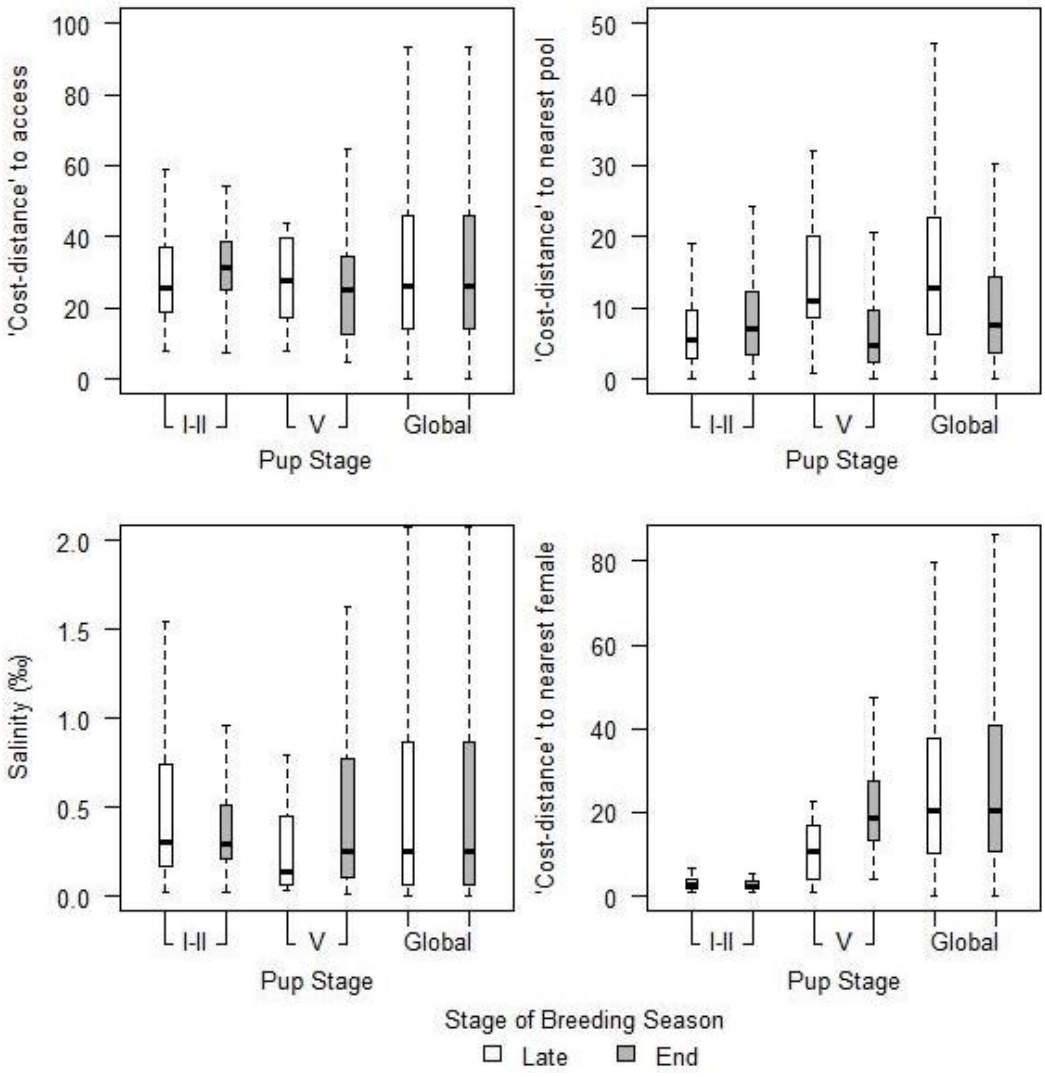

Figure 5.5: Stage I-II (neonate) and Stage V (weaner) pup distributions on CACC, CPOOL, SAL and CFEM for both focal dates, compared with the global EGV distributions. See Figure A4.2 for a plot including outliers.

Hurlbert's niche breadth index, *B'*, indicates that both neonates and weaners have relatively broad niches on most of the EGVs considered (Table 5.6). Interestingly, neonates have a very restricted niche with regards to CFEM, especially compared to that of weaners (Table 5.6). This, alongside an assessment of the mean CFEM value, indicates that neonates occupy sites close to their nearest adult females, and are rarely found in sites far from females, which makes good biological sense. The niche breadth of weaners on the EGV CACC increases between breeding

season stages, indicating the use of sites over a wider range of distance to access, though the opposite is true of neonates. The range of CPOOL values occupied by both neonates and weaners also increases over the season, which seems to occur as a result of more weaners moving closer to pools over the season (Figure 5.5) and proportionately more neonates being found further from pools as the season progresses (Figure 5.5). It is therefore apparent that the niche of weaners is differentiated from that of neonates primarily by their respective 'preferences' for distance to females and to access points.

Table 5.4: Niche overlap of weaners and neonates on focal dates during 2010. Overlap assessed using Pianka's niche overlap index. CACC: 'Cost-distance' to access; CPOOL: 'Cost-distance to nearest pool'; CFEM: 'Cost-distance' to nearest female.

EGV	Stage of Breeding Season	
	Late	End
CACC	0.459	0.532
CFEM	0.673	0.088
CPOOL	0.544	0.909
Salinity	0.798	0.790

Table 5.5: Summary of the discriminant factor on both focal dates in 2010. EGV coefficients show which EGVs are preferred by each age group. Positive coefficients show that high values of this EGV favour the neonates, whilst negative coefficients show that high values of the corresponding EGV are favoured by weaners. CACC: 'Cost-distance' to access; CPOOL: 'Cost-distance to nearest pool'; CFEM: 'Cost-distance' to nearest female.

	Stage of Breeding Season	
Discriminant Factor	**Late**	**End**
Eigenvalue	29.385	17.847
Explained Variance	88.8%	82.3%
EGV Coefficients		
CACC	0.318	0.673
CFEM	-0.524	-0.666
CPOOL	-0.452	0.308
Salinity	0.648	0.093

Table 5.6: Niche breadth of weaners and neonates on focal dates during 2010. Niche breadth assessed using Hurlbert's niche breadth index. CACC: 'Cost-distance' to access; CPOOL: 'Cost-distance to nearest pool'; CFEM: 'Cost-distance' to nearest female.

Pup Stage	EGV	Stage of Breeding Season	
		Late	End
Neonate	**CACC**	0.514	0.436
	CFEM	0.136	0.071
	CPOOL	0.545	0.780
	Salinity	0.574	0.508
Weaner	**CACC**	0.265	0.598
	CFEM	0.366	0.588
	CPOOL	0.488	0.682
	Salinity	0.654	0.608

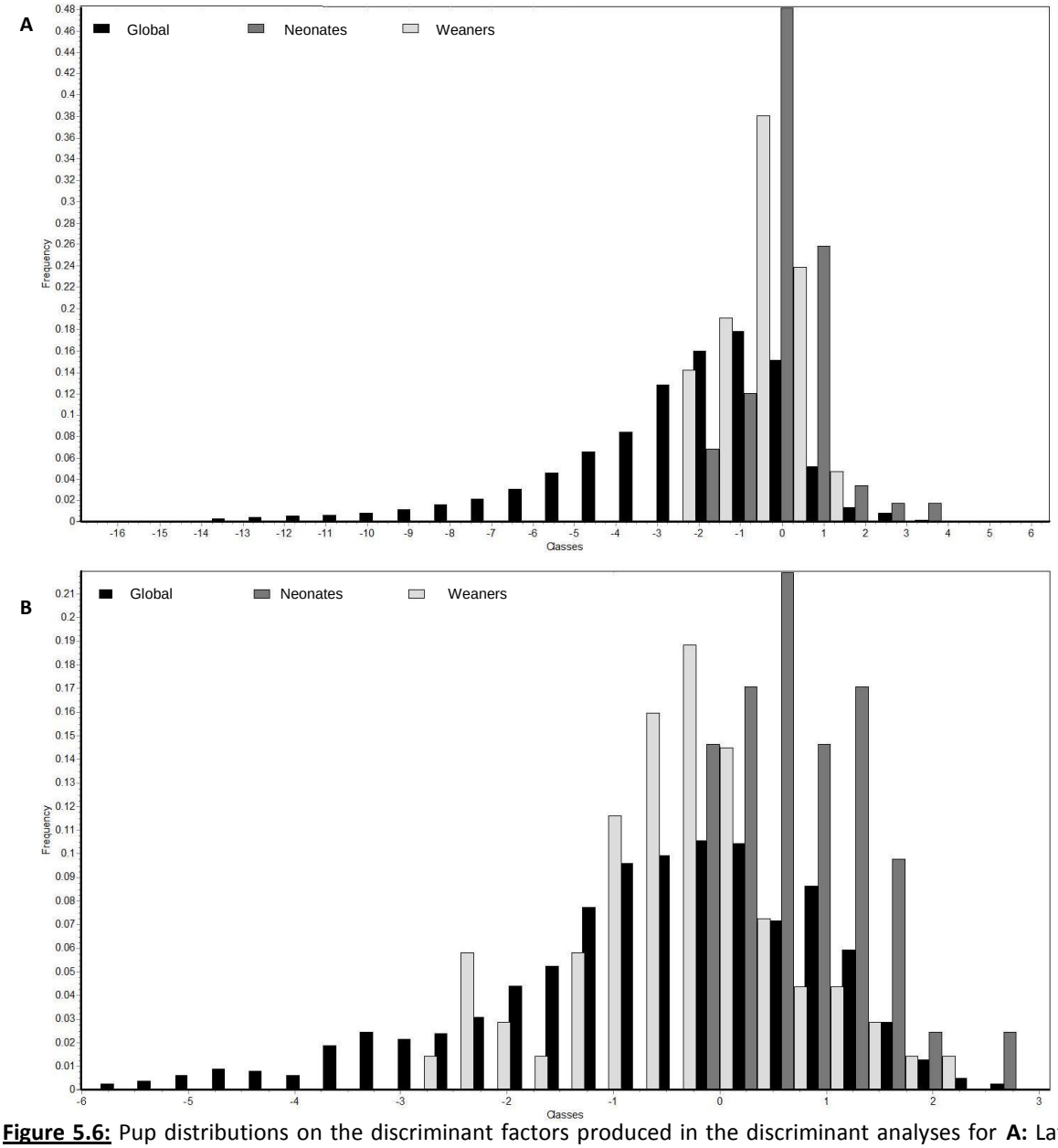

Figure 5.6: Pup distributions on the discriminant factors produced in the discriminant analyses for **A:** Late 2010 and **B:** End 2010. In both cases, weaners are classified as the 'negative age class'.

5.4 Discussion

Both neonates and weaners show significant clustering, though become less aggregated over the season. As the initial position of pups is determined by the mothers, this is unsurprising, as female aggregation shows a similar trend (Section 3.3.3). Though weaners also appear to become less aggregated over the season, the relationship between nearest neighbour index (*R*) and day of breeding season (Figure 5.2) is less well defined than for neonates (Figure 5.2) or females (Section 3.3.3; Figure 3.17). A visual inspection of the distribution maps (e.g. Figure A4.1) shows that although weaners disperse more over the season, there appears to be a tendency for small clusters, or 'gangs' of weaned pups to form, which supports previous observations (PPP and SDT, *pers. comm.*). This clustering may indicate a degree of sociality amongst the weaners which, given the benefits often associated with sociality (Axelrod and Hamilton, 1981; Ferriere and Michod, 1996), might contribute to longer-term pup survival. It would therefore be interesting to

investigate the potential for longer-term associations amongst weaners in these clusters after the PWF. However, the limited available evidence suggests that pups do not associate closely when they leave the colony (Hall *et al.,* 2001). An oft-cited cause of group formation is predation avoidance (Alcock, 1993; Krebs and Davies, 1995), which may provide an alternative explanation for the formation of these clusters of weaners. It may be that small groups of pups are less vulnerable to attack from gulls than solitary individuals, though gull attacks on weaners are rare (SDT *pers. comm.*). A more prosaic explanation is that this could simply be the result of convergent locomotion to limited areas not occupied by adults, possibly preferentially to areas that provide shelter from the wind and driven rain (Kovacs, 1987).

Niche breadth and overlap indices, alongside the discriminant analysis, indicate that in 2010 weaners were found closer to access points and pools as the season progressed, but further from adult females. This suggests that they occupy areas around pools that are as yet uncolonised (or have been abandoned) by females. Weaners are significantly further from females than are neonates throughout the season, with increasing distance as the season progresses; the niche overlap index for CFEM indicates that not only do the neonates and weaners differ in CFEM values on average but that there is very little overlap between niches, suggesting that it is very rare for a weaner to remain in close proximity to an adult female. These analyses suggest that distance to nearest adult female is the site characteristic on which neonates and weaners most differ in their distribution, suggesting that given a choice of sites of equal CPOOL, Salinity and CACC, weaners are likely to choose those a reasonable distance from adult females; the likely reasons for this are discussed below. Given the preferences of females for pupping sites at intermediate distances to access points and pools, it is unsurprising that weaners are found closer to access and pools than neonates. In fact, CACC appears to be important for distinguishing neonate and weaner niches, with weaners being found closer to access, on average, as the season progresses. The decrease in mean CACC value for weaners over 2010 suggests overall movement towards the sea, though it seems likely that in reality weaners are simply moving into areas less preferred, or previously vacated, by females, possibly as an adult avoidance strategy. This is because weaner niche breadth on the EGV CACC increases over the season, rather than simply staying constant or decreasing as all weaners move towards the sea; indeed, Figure 5.5 shows that not all weaners are moving towards access points. This makes sense as weaners typically do not venture out to sea for the first time until after a substantial terrestrial PWF (Coulson and Hickling, 1964). A visual inspection of pup distribution maps appears to support this (Figure A4.1); furthermore, Chapter 3 showed that late arriving adult females colonise further inland away from access points as the season progresses. The degree of inland colonisation by adult females may, therefore, dictate the distance travelled, and site chosen, by weaned pups attempting to avoid these females.

Neonates are found in less saline areas as the season progresses, whilst weaners are found more often in sites of higher salinity. Though statistically significant for weaners, the differences in mean salinity at pup locations between breeding season stages are so minute that it seems unlikely that they are biologically significant, or relevant. As discussed in Sections 3.4 and 4.4, it is likely that, due to the salinity surface interpolation method, such small differences are caused by a change in pup proximity to pool. Indeed, neonates are found further from pools later in the season, whilst the opposite is true for weaners (Figure 5.5). Despite this, pups clearly avoid high salinity sites; although Reilly (1991) found that pups did not dehydrate during the PWF, there was evidence for a negative water balance, so it may be that pups drink from pools to address this. As suggested in Section 4.4, manipulative or natural experiments are required in order to reliably determine whether seals drink from pools of water to achieve or maintain a positive water balance, though the results presented here, combined with observations of individuals drinking, indicate that this may be the case. Given the large distances between weaners and their nearest adult female (Figure 5.3; Table 5.3) and the shorter distances between adult females and their nearest pool (Chapter 4), it is likely that weaners, which remain close to pools, are closer to pools on the outskirts of the colony that remain largely unused by the females. This is supported by observations of pup behaviour (SDT, *pers. comm.*) and by visual inspection of pup distribution maps (Appendix 4, Figure A4.1), and may become easier towards the end of the season, when fewer females are ashore and more pools are available.

The results presented here support observations suggesting a tendency for weaned pups to avoid the main areas of the colony (e.g. Boyd *et al.,* 1962; Kovacs*,* 1987) which have the highest adult density (Pomeroy *et al.,* 1994), and may aggregate near pools in areas close to sheltered access gullies (Kovacs, 1987). It is likely that this pattern of site use by weaned pups is a result of aggressive interactions with adults; a number of researchers have observed pups being driven out of areas occupied by lactating females (e.g. Kovacs, 1987). These aggressive interactions may be particularly pronounced soon after weaning if pups attempt to suckle from non-maternal females. These females display high levels of aggression towards potential threats to their pups, and this aggression, as a form of protection, is important to pup survival and to prevent milk theft (Boness *et al.,* 1982). Further studies on weaner space use should also account for the presence of adult males; this could be achieved using a similar surface to the CFEM surface.

Adult male presence is likely to influence weaner space use because pups may also be in danger of trampling or being otherwise subjected to aggressive interactions with adult males; this is certainly the case for northern fur seal (*Callorhinus ursinus*) pups, which suffer increased mortality as the breeding season progresses due to an increase in attacks by sub-adult males (Kiyota and Okamura, 2005). The dangers associated with this are likely to increase over the season as more adult males come ashore and therefore levels of male-male and male-female

aggression increase (Twiss, 1991) as males attempt to gain matings. As female distribution largely determines the distribution of males (Twiss *et al.,* 1994, 2007), these aggressive interactions are likely to occur with greater frequency, and possibly intensity, around areas of higher female density, for example with dominant males chasing transients from 'their' females. Therefore, the distribution of pups observed here may also be a result of the distribution of males and aggressive interactions on the colony. The collection of behavioural data alongside fine-scale distribution mapping could also help to address the importance of aggressive interactions in determining seal distributions, as highlighted by Twiss *et al.* (2003). For example, collection of all-occurrence aggression data in the few hours prior to individual distribution mapping could assist in teasing apart biotic and abiotic influences on the habitat use of both females and pups, though more frequent mapping (>1 day^{-1}) of all sex/age classes is unlikely to be feasible in a colony of this size.

The differences in neonate and weaner habitat use highlight the importance of treating stage classes differently when it comes to assessing resource use. This also provides support for the approach used throughout this thesis, which limited the locations classed as pupping sites to the very earliest (Stage I-II) pup stage classes, rather than including all pup locations as pupping sites. It is likely that markedly different conclusions would have been reached in Chapters 3 and 4 if all pups had indiscriminately been used to indicate pupping site choice; in particular the niche breadth would have appeared substantially greater, likely causing a reduction in observed 'specialisation' (an increase in the 'tolerance' of neonates for a wide range of conditions).

As outlined in Section 5.1, an extended PWF depletes the energy reserves of grey seal pups, with approximately 94% of the energy consumed derived from lipids (Reilly, 1991). A trade-off must therefore be made between attainment of high physiological conditioning prior to leaving the colony and maintaining sufficient energy and insulation for foraging in a cold marine environment. A direct link has been made between post-weaning survival and condition at weaning (Hall *et al.,* 2001), with fatter pups achieving greater probabilities of first-year survival. Post-weaning, the resources available to the pup are limited until the first successful foraging attempt, so the duration of the PWF and the activities engaged in during the PWF may have a tangible influence on first-year survival through blubber depletion, especially as relatively small changes in pup size have been suggested to have a large effect on survival probability (Hall *et al.,* 2001). Therefore, though locomotion towards areas of low adult density may initially appear energetically expensive, the subsequent avoidance of injury risk and energetically expensive aggressive interactions with multiple adults may contribute substantially to retaining vital energy reserves and thus to first-year survival. The number of available sites with low adult density, which is likely to be determined by the available range of EGVs at each site (Chapter 4), may therefore have a substantial effect on post-weaning pup mortality and subsequent recruitment and colony growth rates. The ease of ultimate access to the sea for weaners is likely to be

especially important, as if weaners at North are 'driven' far inland it could be costly for them to reach the sea, compared to individuals at sites with more open access such as the Monach Isles.

This study provides a better understanding of the implications associated with multiple grey seal age classes sharing a finite environment, indicating potential exclusion of weaners from areas favoured by adult females. Just as evasive strategies may develop between ecologically similar sympatric species, resulting in decreased competitive interactions and more stable coexistence (Lisičić *et al.,* 2012), the same may be true of conspecific age classes, as appears to be the case here, allowing stable coexistence within the limited space afforded by inland island breeding colonies. This study could be extended to assess the habitat preferences of adult male grey seals, using the four EGVs included in this chapter within an ENFA model, or similar, to assess the importance of female distribution relative to abiotic factors. Female distribution may initially appear relatively unimportant, but this will likely change as more females come into oestrus over the course of the season and more males compete to gain access to sites near to females. However, the polygynous mating system of the grey seal complicates the use of this simple approach: the importance of proximity to females will likely be distorted by male-male dominance relationships, which will force transient males to use sites much further from females than they might otherwise prefer. In addition, the 'strategy' employed by individuals males may be important, as often males that 'defend' female groups from early in the season before the females come in to oestrus are more successful than later-arriving males (SDT *pers. comm.*), making the temporal aspect of site choice more complex. In this case it may be best to assess the site use of tenured, dominant males separately from transients, or investigate individual-based approaches which account for relative dominance.

6. General Discussion

6.1 Key findings and conclusions

Using a purely hands-off observational approach, this research has addressed the main aims set out in Section 1.5. Firstly, in Chapter 3, it is noted that the colony has experienced a substantial decline in number of females and pups between 1998-2010, with no notable effect on breeding density (degree of aggregation) *between* seasons, though the distribution of females and neonates changes dynamically on a daily basis as a result of individual movements and breeding female turnover (i.e. new arrivals to the colony and early-pupping females leaving) over the course of a season. This change results in progressive inland spread and in a change in distribution of seals relative to one another. Generally adults become less densely aggregated over the season, but maintain a similar distance to their pups. It is also clear that the weather patterns on North Rona are highly variable and unpredictable, both within and between years.

This research represents the first application of an integrative modelling approach utilising all known influential habitat features to the terrestrial site preferences of female grey seals; it is also novel in using EGV data at a temporal scale that corresponds very closely to the distribution data, making use of remotely sensed pool distribution data to quantify the breeding habitat at a very fine spatial and temporal scale. In taking this approach, this research has confirmed previous ideas regarding the influences of the breeding environment on their site use. Chapter 4 demonstrated that females prefer pupping sites and habitat at intermediate proximity to pools and access points to the sea. This corroborates previous qualitative observations that pool availability is an important determinant of female distribution (Boyd *et al.,* 1962; Anderson *et al.,* 1975; Pomeroy *et al.,* 2000a; Twiss *et al.,* 2000a; Redman *et al.,* 2001; Twiss *et al.,* 2002*,* 2007) and that intermediate proximity to access is also important (Pomeroy *et al.,* 1994), though generally sites immediately next to access gullies are typically less favoured (likely as a result of the high 'traffic' in these areas, which act as thoroughfares for females joining or leaving the colony form the sea; Twiss *et al.,* 2003; Stephenson *et al.,* 2007). The preference for proximity to pools of water is likely to be a result of the tendency for females to bathe in these pools to maximise heat loss, which "is likely to be the most efficient method for dissipating excess heat because of the high cooling capacity of water (Øritsland *et al.,* 1978; Campagna and Le Boeuf, 1988; Riedman, 1990)" (Twiss *et al.,* 2002: 465). Though it has been confirmed previously that female grey seals use the pools of water as a means of behavioural thermoregulation (Redman *et al.,* 2001; Twiss *et al.,* 2002), this research is novel in also quantitatively demonstrating that females show a clear preference for pools of low salinity. The only plausible explanation for this is that the seals are using pools to drink, as well as for thermoregulation, providing quantitative support to previous observations (PPP and SDT, *pers. comm.*) of seals drinking from pools.

Chapter 4 also identified subtle differences in pupping site and subsequent habitat choice of female grey seals, demonstrating that pupping sites are typically further from access points and from pools than the sites subsequently used by the females themselves. It is concluded that this represents a sort of female strategy, whereby a mother will leave her pup in sites less preferred by adult females, and commute to a more suitable area closer to a pool, whilst the distance between pupping site and subsequent habitat is likely to be determined by how individual females address this 'pup-pool' trade-off. In examining site preferences at multiple points within each season, this research has also demonstrated that the pupping site and habitat preferences appear to change over each season as females and neonates are found more often in more 'average' sites. This may occur as a result of preferential colonisation of more favoured areas by early-breeding females that subsequently exclude other females from these areas, causing them to select less favoured sites (Section 4.4). Alongside this is a general progression towards pupping sites further inland, as reported by previous researchers (Anderson *et al.,* 1975; Kovacs, 1987; Twiss *et al.,* 2000a, 2001). Indeed, Stephenson *et al.* (2007) found that the majority of pups born later in the season were found more than 30m from access on the Isle of May, which was taken as evidence that late-arriving females choose not to occupy sites at more intermediate distances to access made available by departure of previous females.

Not only is this research the first to assess the impacts of key EGVs simultaneously, as opposed to taking a hierarchical approach to the study of grey seal habitat preferences (Twiss *et al.,* 2000a), but is also the first to take a multi-annual approach to this issue, using EGV data from the same time period as the seal presence data, whereas previous research (Twiss *et al.,* 2000a) has been performed using pool distribution data from the 1994 breeding season. This updated approach has addressed the question of how patterns of site use change over multiple seasons with regards to changes in EGV availability, and, by extension, weather patterns. This multi-annual approach has demonstrated an apparent surplus of suitable habitat in each year, suggesting that declining pupping site or habitat availability is not contributing to the decline of the North Rona colony. It has also demonstrated relative consistency in site preferences between years. Of course, it is important to bear in mind that female grey seals can breed for many years, from reaching maturation at three to five years of age up to around 42 years of age (Hewer, 1960; Pomeroy *et al.,* 1999; Worthington Wilmer *et al.,* 1999; Bowen *et al.,* 2006), so even this research, which spans a period of 13 years, only shows the population preferences over a relatively short time frame. The extensive photo-ID catalogue for females at North Rona, in conjunction with rapid developments in automated photo-matching software (Hiby *et al.,* 2012), may be useful in tracking the habitat and pupping site choices of individual multiparous females over a longer time frame. This could identify any inter-annual changes or consistencies in site use and potentially relate these to metrics of individual fitness or reproductive success.

Chapter 5 utilised an alternative approach to Chapter 4, and in doing so highlighted the subtle differences in site use of independent, weaned pups relative to that of neonates. It was discovered that weaned pups were found in sites much further from adult females than neonates were, and that the distance between these weaners and adult females increased throughout the breeding season. This appears to be achieved by weaner movement away from areas preferred by adult females and into areas closer to access, though weaners manage to maintain proximity to pools of standing water. It is likely that they move into areas that are as yet uncolonised by females, or that have been abandoned by previous females and not re-colonised. It was concluded, in line with previous observations at North Rona (PPP and SDT, *pers. comm.*) that this is likely to be a strategy for avoiding aggressive interactions with adult seals, which might otherwise pose a substantial threat to weaner wellbeing. Throughout the 2010 season, weaners also became generally less aggregated at the scale of the SS, though formed small 'gangs' which may be related to either social tendencies or predator avoidance (Section 5.4).

The detailed relevance of these findings for grey seal ecology, including related caveats, has been discussed in the relevant chapters (Chapters 3 through 5). The remainder of this chapter will consider the broader issues surrounding the methodology used throughout this thesis (Section 6.2) and the broader relevance of the results in terms of other grey seal colonies (Section 6.3.1) and other pinniped species (Section 6.3.2). Section 6.3.3 will then consider the broader effects of female distribution on pinniped ecology, before Section 6.4 outlines potential further extensions of this work. The final conclusions are then presented in Section 6.5.

6.2 Methodological considerations

6.2.1 Statistical comparison of multiple groups

Deciding on a statistical test to apply to multiple comparisons of means is often challenging, particularly where an appropriate test may not be readily available from the statistical literature (Herberich *et al.,* 2010). This is especially true when the data exhibit heteroscedasticity, because common post-hoc multiple comparison tests such as Tukey's (Tukey, 1953) and Dunnett's (Dunnett, 1955) assume homogeneity of variance amongst all treatment (and "control") groups. Violating this assumption when using such tests can result in a high probability of a Type I error. The choice of an appropriate test becomes further limited when sample sizes are unbalanced amongst the groups and/or the data are non-normal. Such problems cannot always be overcome by data transformations (as multi-normality might only be achieved by application of different transformations to each group), or by switching to non-parametric tests, which still assume that the distributions of data in all groups have the same shape, implying equal variance (Hollander and Wolfe, 1999). MULTCOMP, a recently introduced framework for multiple comparisons of means under non-normality and heteroscedasticity (Hothorn *et al.,*

2008), has been used throughout this thesis for multiple comparisons of means where such problems have arisen. Though several approaches have been reported for comparing multiple means under heteroscedasticity (Weerahandi, 1995; Lee and Ahn, 2003; Xu and Wang, 2008), MULTCOMP was chosen as it is the only approach which can also test for differences in means between groups with unequal sample sizes. MULTCOMP makes no assumptions regarding the shape of the distributions, sample sizes or variance homogeneity, and previous researchers have demonstrated that MULTCOMP performs well with data that are heteroscedastic and non-normal, with unequal sample sizes. It was therefore especially useful when comparing the species EGV means (sample sizes ranging from 19-418) with the global EGV means (sample size = 82223).

6.2.2 Ecological Niche Factor Analysis

The freely available software BioMapper 4.0 (Hirzel *et al.,* 2002) was used to perform the Ecological Niche Factor Analyses in Chapter 4. The presence data utilised spanned a range of sample sizes (19-418); despite this, trends in habitat preferences identified by this method were fairly consistent and showed some interesting and explicable trends. These trends are unlikely to be statistical effects of the differing sample sizes, since ENFA has been shown to be insensitive to changes in sample size, at least when it comes to modelling HS (Zaniewski *et al.,* 2002; Sattler *et al.,* 2007). Furthermore, Kadmon *et al.* (2003, 2004) found that a similar PO approach (climatic envelope modelling) performed well with 50-75 presence points, a 'threshold' reached in all but two focal days (females and neonates at the beginning of 2010 and neonates at the end of 2010). Furthermore, some recent work has achieved good results despite much lower sample sizes (e.g. Rutishauser *et al.,* 2012). The only instance in which sample size appeared to be a problem throughout this research was in ENFA computation for neonates (n=19) for the beginning stage of 2010. In this case, very large eigenvalues were computed as a result of low variance among species sites and the analysis was taken no further. Generally however, ENFA is thought to work well provided that it is computed with at least 3 times as many presence points as EGVs (Hirzel, 2008). The sample size for each ENFA iteration may be improved by including more than one day's worth of presence data, from the days preceding and following the 'focal' day. However, this was not carried out due to uncertainty in the change in pool distribution resulting from variable rainfall. Some focal days were preceded or immediately followed by heavy rainfall, whilst others remained dry; this means that the seal locations on these days would likely be responding to unquantified changes in the environment and it was, therefore, deemed inappropriate to include further presence data.

A potential problem with the ENFA approach, alluded to in Section 4.4, regards the use of presence data to define suitable habitat. This is a problem common to all SDM approaches, and may be summarised as follows. Individuals may occasionally be found outside of what may be

considered as their niche (Pulliam, 2000) in areas that may sustain them in the short term but that present conditions which cannot provide reproductive success (Guisan and Thuiller, 2005). Examples of this are widespread, with substantial support for such occurrences provided by ecological theory regarding ecological traps and source-sink dynamics (Pulliam and Danielson, 1991; Dunning *et al.,* 1992; Kristan, 2003). Such presence data could therefore decrease the resolution with which modelling approaches can delineate suitable conditions and habitat preferences. This issue is relatively easily identified, though presents a major challenge in formulating solutions, and is rarely addressed (c.f. Railsback *et al.,* 2003; Olsen *et al.,* 2004; Titeux *et al.,* 2007). As alluded to in Section 4.4, demographic and/or reproductive parameters are more likely to provide a good estimate of the suitability of a site than simple presence or absence (van Horne, 1983), and so the relative success of individuals at a particular site may be a better indicator of its suitability (Titeux *et al.,* 2007; Mosser *et al.,* 2009; Gaillard *et al.,* 2010). However, it is currently possible that the inclusion in the ENFA of unsuccessful females residing in locations outside of the species niche gives rise to an incorrect evaluation of species marginality and an underestimate of the specialisation of the species (i.e. an overestimate of niche width), potentially masking a decline in overall HS of North Rona over the last two decades. Titeux *et al.* (2007) found that incorporating reproductive success parameters in ENFA modelling indicated that successful female red-backed shrike (*Lanius collurio*) were more selective in choosing their nest site than was indicated by a model which did not take reproductive success into account. Therefore, this may be a more appropriate approach to ENFA than simply assessing HS based on seal presence, particularly as topography has been implicated as a cause of pup mortality (Boyd *et al.,* 1962; Coulson and Hickling, 1964; Sumers *et al.,* 1975; Twiss *et al.,* 2003).

This problem is particularly challenging to address for grey seal pupping site and habitat preferences, as reproductive success is difficult to assess from the available data (i.e. aerial photographs and location maps). As topography has been implicated in pup mortality rates (Twiss *et al.,* 2003), the presence of dead pups could be used as an indicator of poor site quality, thus negating the effects of inclusion of females in the model that pup in locations outside of the suitable habitat. However, this would likely be a poor indicator of poor quality habitat, not least because abandoned pups often wander far from their natal site before death (Twiss *et al.,* 2003), and pup mortality is likely influenced by other, unquantified factors (Anderson *et al.,* 1975; Baker, 1984, 1988). In addition, the majority of pup deaths occur post-weaning during the first year at sea (Harwood and Prime, 1978; Twiss *et al.,* 2003). Due to the difficulty associated with tracking individual pups their mortality is difficult to measure on a large scale, and therefore almost impossible to also correlate with the nursing environment. Typical metrics of reproductive success in grey seals include maternal mass transfer efficiency and pup mass gain, growth rate and weaning mass (Lydersen *et al.,* 1994, 1995; Pomeroy *et al.,* 1999), and are available for a number

of individuals which form part of a long-term study of reproductive success at North Rona. Many of these metrics may be influenced by breeding colony topography (Redman *et al.,* 2001; Twiss *et al.,* 2003) and may therefore provide an excellent means to link pupping site environment with reproductive success, though of course individual differences in maternal quality will also likely account for a lot of the variance in reproductive success (Twiss *et al.,* 2012). For example, Pomeroy *et al.* (2001) provided evidence of high growth rates of pups and potentially increased genetic success for mothers occupying 'prime' habitats such as those identified here, hinting towards the potential success of this approach for grey seals. However, this alternative approach to assessing HS could only be applied to a subset of the individuals pupping at North Rona each year, as, not only are there logistical difficulties with collecting these measures of reproductive success for all or even most of the females throughout the colony in each season, but significant ethical concerns associated with the disturbance that this would cause within the colony.

Unfortunately the ENFA approach would not be capable of incorporating *relative* reproductive success, so a "success threshold" to distinguish successful *versus* unsuccessful individuals would have to be determined in order to eliminate unsuccessful mothers from the input presence data. Alternatively, the locations of unsuccessful mothers could be incorporated as a form of 'absence' data in a PA model, to provide an indication of unsuitable habitat. However, as noted in Section 4.1.1, it has been argued that methods utilising PO data are more useful than PA approaches for describing the fundamental niche of the focal species (Zaniewski *et al.* 2002); ENFA may therefore still be preferable, especially as unquantified biotic interactions (discussed in greater detail in Sections 6.2.4, 6.3.1 and 6.3.2) might influence the success of individuals in certain locations independently of the environmental conditions.

The final issue associated with using *female* locations as indicators of habitat preference is that some females will not have a pup, whilst those that do will have pups of different ages. Given the change in metabolic cost associated with lactation (Reilly *et al.,* 1996), a female's reproductive status could have dramatic implications for her resource preference, particularly with regards to proximity to pools. Lactating females, which necessarily have increased BMRs, are likely to prefer to be nearer to water for thermoregulation, and for drinking to address the negative water balance incurred during this terrestrial phase. Therefore, the inclusion of all females in the presence data may have masked the preferences of nursing mothers. The approach to assessing female habitat requirements used throughout this thesis has therefore addressed the habitat preferences of all adult females; future work to delineate the habitat preferences of nursing mothers could limit the presence data to those females known to have neonates (though this would require extensive daily observations on mother-pup pairs to determine pup age and maternal affiliation) throughout the breeding season. Furthermore, the behavioural contexts of females without pups and females with older or younger pups are likely to be different (Redman

et al., 2001; Twiss *et al.,* 2007). This will likely affect female movement patterns and the pup-pool trade-off discussed in Section 4.4. For example, females with older pups are likely to be thinner and, therefore, may not require water for thermoregulation, though may be influenced by male behaviour as they come into oestrus. Meanwhile, the behaviour of early lactation females may be restricted by the greater need for proximity to their pups, which are highly dependent on maternal attention for protection (Kovacs, 1987).

To compare female and neonate niches in Chapter 4, the results of the ENFA for females and neonates were directly compared. There has been increasing scrutiny of the utility of comparing species distribution models and similar as a surrogate for directly comparing the environmental requirements of a pair of species, or conspecific age classes (Elith and Graham, 2009; Godsoe, 2010; Godsoe, 2012). This method, in widespread use (e.g. Peterson *et al.,* 1999; Broennimann *et al.,* 2007; Warren *et al.,* 2008; McCormack *et al.,* 2010), has been criticised as being of unknown reliability and for generally being biased towards identifying substantial differences between niches (Godsoe, 2012). The predominant reason for these criticisms is that such a method is prone to confusing changes in global availability of predictor variables (EGVs) with changes in requirements between species. However, this assumes that the species (or age class) distributions were assessed in separate areas with distinct environments available to each group. The approach used throughout this research has assessed female and neonate distributions relative to a set of EGVs within a predefined SS, only comparing requirements of these age 'classes' within a single focal date. Thus, the criticisms levelled at this approach do not apply in this instance, and my approach retains its validity in this respect. The same applies to the discriminant analysis approach utilised successfully in Chapter 5. The only unquantified aspect of an individuals' environment in this research that might influence the results of female and pup models differently is biotic interactions; this is explored further in Section 6.2.4.

6.2.3 Differences in the spatial and temporal resolution of the EGV and species data

The findings of this research reveal several key issues which apply to all SDM approaches, which were raised in Chapter 1 (Section 1.4). The EGV maps utilised in this research demonstrate the very fine scale at which the topography on North Rona varies. Given that the subsequent HS maps also vary spatially and temporally at such a fine scale, with consequent effects on seal distribution, modelling the habitat at the grain and extent at which it is experienced by an individual is clearly a valuable approach; this fact is becoming increasingly recognised throughout the literature (Twiss *et al.,* 2000; Bowyer and Kie, 2006; Loe *et al.,* 2007; Aublet *et al.,* 2009; van Beest *et al.,* 2011). It is known that coarser scales may yield different and inaccurate outcomes (e.g. Lowe *et al.,* 2010). Therefore, when analysing distribution data collected at a scale as fine as that in the current study it is important to maintain, as far as is possible, a similarly fine temporal

and spatial scale in the EGV data, especially given the rapid and plastic responses to a changing environment exhibited by many species (e.g. Charmantier *et al.,* 2008; Moyes *et al.,* 2011; Tuomainen and Candolin, 2011; Salido *et al.,* 2012). Furthermore, ENFA combined with the fine scale variation in EGVs and HS has implications for the generality of models such as those created here (Guisan and Zimmerman, 2000; Sattler *et al.,* 2007). Models of HS are only truly valid if built using distribution and EGV data from the same time frame. For the creation of SDMs which are more applicable over a wider time frame it would be advisable to monitor the EGV distributions at a coarser scale, as such measurements typically show less change over time, sacrificing accuracy and precision for generality. Models created with EGV distributions measured at a very fine scale are therefore very specific to the time frame from which EGV data were collected, and subsequent fine scale changes in EGVs (such as CPOOL) over time limit the application of these models to distribution data collected even a few days apart.

In terms of the temporal resolution of the data, CACC and ELEV are invariant over time, whilst CPOOL data from aerial photographs were utilised in such a way that they could be associated to daily presence data from the same day. The salinity data is the only dataset that was collected at a different temporal resolution (Chapter 2), being a composite of data collected over several days near to the focal days in 2009 and 2010. Though measured at a slightly coarser temporal scale, the salinity data were collected in such a way that it was possible to demonstrate change in SS salinity over each season, allowing quantification of change in availability of environmental conditions.

6.2.4 Alternative predictor variables with potential effects on seal distribution at North Rona

In Section 4.4, the potential influence of conspecific interactions on the ENFA models were identified. This will be considered in greater detail here, though is a factor that is likely to be influential at (though may vary between) all colonies, and in all colonially breeding pinnipeds. If this work is to be extended to other sites further factors will also need to be considered, and these are outlined in Section 6.3.1. As shown in Chapter 3, the distribution of females changes dynamically on a daily basis as new females arrive, likely causing local fluctuations in density. Additionally, the highly variable weather patterns contribute to changing distributions of EGVs known to influence female distribution. Whilst the change in EGVs has been shown to influence the dynamic change in female distribution, the distribution of females is in itself likely to influence the distribution of new arrivals. Stephenson *et al.* (2007) suggested that social factors, including aggression, may influence female habitat choice; this is based on the knowledge that breeding females behave towards conspecifics in an intolerant manner that could regulate breeding density (Anderson *et al.,* 1975; Kovacs, 1987; Pomeroy *et al.,* 1994), protecting their pups by displaying aggression towards conspecifics that approach within 2 body lengths (4-5m) following parturition

(Pomeroy *et al.,* 2000a). As the distribution of females changes throughout the season, the potential levels of aggression at a particular site will also vary dynamically across the season. Stephenson *et al.* (2007) proposed that it is, therefore, important to include factors such as conspecific aggression in any model of grey seal distribution, but found that their approach to modelling both topography and aggression did not improve upon a topography-only model of pupping site use at the Isle of May. However, their approach did not incorporate adult female or male presence, but modelled aggressive interactions as a function of pup presence. The present study demonstrated that females are rarely directly next to their pups, whilst it is known that not all females will have a pup at a given moment as some may have weaned their pup or may still be pregnant. It would, therefore, be beneficial to instead model the probability of aggressive interactions as a function of the presence of adult males and females, or even include observations of aggressive interactions recorded in the field, which may better represent the distribution of aggression across the colony than the distribution of pups. As mentioned in Section 4.4, in addition to limiting site choice through aggressive interactions, conspecifics could represent barriers to movement which would complicate the application of 'cost-distance' surfaces used in this research. It would therefore be useful to incorporate conspecific presence and aggressive interactions within a distribution model, though the highly variable nature of these interactions would make this approach very difficult to implement at the population level, meaning an iterative individual-based approach would be required.

The incorporation of these conspecific interactions is further complicated by individual differences in experience, behaviour and condition. For example, some (older, more experienced) females (and certainly males) may be more dominant than others and better able to acquire and maintain their position at high quality sites (Pomeroy *et al.,* 1999; Twiss *et al.,* 2000). The distribution of dominant and subordinate individuals is likely to influence the fine scale distribution of aggressive interactions, and therefore affect the site choice of late-arriving females. Furthermore, previous research has uncovered the potential for social associations between females (Pomeroy *et al.,* 2005; Ruddell *et al.,* 2007), which could further obscure the effects of aggression on models of space use. Social associations between familiar individuals could lead to reduced aggressive interactions within these groups, meaning that areas in which they are found might appear to have low levels of aggression when assessed by behavioural observations. These areas may, therefore, appear more suitable to new arrivals; indeed, a link between individual associations and habitat quality has been made previously, in a theoretical paper by Pepper and Smuts (2002). The authors argue that non-random cooperative associations can occur so long as individuals are more likely to leave low quality than high quality environments, and a cooperative trait exists that affects local environmental quality. In other words, non-random associations based on cooperation or reduced aggression could feasibly

contribute to increased suitability of a site amongst familiar females. However, a 'new' or 'foreign' female entering the vicinity of these females may experience much higher levels of aggression than expected based on previously observed levels of aggression, which will influence her site choice and obscure the results of the model.

These socially structured female groupings may arise as a result of the site fidelity exhibited by female grey seals (Pomeroy *et al.,* 2000b), through inter-annual return of largely similar groups of females to approximately the same site and potentially through use of the island as a summer haul-out, which may reinforce breeding associations (Pomeroy *et al.,* 2005). Therefore, younger females that have not yet had the opportunity to form social 'bonds' may select pupping sites based more on topography than older females for whom social factors may be important. Creating models similar to those presented here using only presence data from younger females and their pups could therefore be informative in this respect, removing some of the potentially interfering (though clearly important) social influences on female distribution. However, it has also been observed that the older, more experienced (and potentially more 'social') females are typically amongst the first to arrive on the colony and give birth, whilst the younger, inexperienced females arrive on the colony later in the season (PPP and SDT, *pers. comm.*). Given the potential for preferential colonisation of the most favourable sites by the first females to arrive it may be that younger females are prevented from selecting sites based solely on the local topography by conspecific presence and aggressive interactions. In order to remove the effects of social influence on site choice, female distribution earlier in the season could be modelled, when fewer females are shore. The results from the beginning of the 2010 season (the earliest stage in the season monitored) suggest that this would be a productive approach, highlighting the distinct preferences of comparatively more 'marginal' females (i.e. those with higher marginality scores, such as those in early 2010, which show preferences for sites with EGV values further from the SS mean). However, this could not be performed for other seasons due to the limited availability of pool distribution data from aerial photographs, which are not typically collected that early in the season at North Rona. The processes determining site selection are clearly very complex, and the best approach for teasing apart the impacts of these various processes may be long-term behavioural observations on groups of known females. Conspecific interactions are likely to play a major role in the distribution of individuals of any colonially breeding species, and should therefore be taken into account in the application of this approach to other grey seal colonies (Section 6.3.1) and different species (Section 6.3.2).

6.3 Implications of this research for a broader understanding of pinniped ecology

6.3.1 Implications for the grey seal at other colonies

Throughout its range, and even in the UK alone, the grey seal breeds on a variety of substrates, from open, boulder-strewn grass (North Rona; Pomeroy *et al.,* 1994) to sandy beaches (Donna Nook, Lincolnshire (*pers. obs.*) and the Monach Isles (Baker, 1984)), open sand bars (Sable Island; Boness and James, 1979) and exposed rock (Isle of May; Twiss *et al.,* 2000a). Even within these sites, the fine-scale topography can vary substantially, with important implications for female behaviour (e.g. Twiss *et al.,* 2000a). Given the apparent preferences for proximity to water demonstrated here (Chapter 4), and the importance of proximity to water for maternal attendance (Redman *et al.,* 2001) and degree of polygamy (Twiss *et al.,* 2007) it is interesting to note that pools of water rarely form at some of these sites, whilst those pools that do form may be more dispersed than at North Rona (e.g. Donna Nook, *pers. obs.*). As local site topography is clearly an important determinant of grey seal site choice (Chapter 4; Pomeroy *et al.,* 1994; Twiss *et al.,* 2000a, 2001, 2003; Redman *et al.,* 2001), it would be interesting to explore how the varied topography at these other sites influences site use and reproductive success. If nothing else, these differences in topography highlight that the habitat and pupping site preferences identified in this research do simply represent *preferences* rather than absolute requirements, since females at some sites can clearly cope without access to pools. Nevertheless, it would be intriguing to investigate the effect of a lack of pools on female distribution, behaviour and reproductive success, especially at locations with temperatures similar to North Rona which would likely induce thermal stress (Twiss *et al.,* 2002). Given the importance of pools to seals at North Rona, it would be interesting to investigate (a) why seals choose to breed at sites at which pools do not tend to form and (b) the advantage conferred to seals that drink water during lactation compared to those that do not have the option. SMRU conducts aerial surveys at the majority of the grey seal colonies in Scotland, and have accrued an extensive, multi-annual catalogue of aerial photographs for these sites. These could be used to rapidly quantify the topography (Mills *et al.,* 1997) and pool distribution at these colonies and examine the distribution of females and pups relative to these features, as seals of all age classes are visible in these photographs (*pers. obs*.).

The conspecific interactions discussed in Section 6.2.4 will clearly have a similar influence at other sites as at North Rona, albeit modulated by space availability and breeding density. However, if the approach utilised here is to be expanded to other colonies, and perhaps other species, some consideration must be given to additional factors that may influence the habitat and pupping site selection at these colonies, in order to better inform the ENFA (or alternative) models. In addition to conspecific interactions, the influence of heterospecifics must also be considered at some other colonies, though at North Rona the only significant heterospecific

interactions occur between seals and scavenging gulls. Generally, heterospecific interactions may occur in the form of predation or interspecific competition (e.g. for space). For example, grey seals are thought to breed alongside aggregations of hauled out harbour seals (*Phoca vitulina*) at Blakeney Point, UK (52° 58' N, 0° 58' E; Wood, 2006; Skeate and Perrow, 2008). Though grey seals are larger and typically more aggressive and dominant than harbour seals, large and established heterospecific aggregations may influence site use by colonising grey seals. Heterospecific interactions are of particular relevance to other pinniped species, as some breed at sites that are more exposed to terrestrial predators (Section 6.3.2). It is also important to consider the effects of disturbance on pinniped space use, and these are considered in greater detail in Section 6.4.2.

6.3.2 Implications for other pinniped species

The parallels in the ecology of many pinnipeds suggest that the ENFA approach used throughout this thesis could be applied with reasonable success to other pinniped species, using a similar set of EGVs. Indeed, similar results using different modelling approaches have been found in other species; for example, habitat characteristics linked to thermoregulation and locomotory costs were key to the habitat use of all sex and age classes of the Galápagos sea lion (Wolf *et al.,* 2005). Twiss *et al.* (2003, 2007) suggested a role for topography in determining pup mortality and a combination of climate and topography in determining the degree of polygny. Similarly, low breeding densities on the homogeneous and spacious beaches of Península Valdés, Argentina (42° 30′ S 63° 56′ W), are linked to lower aggression and pup mortality in the southern elephant seals at this site compared to other sites, at which the topography imposes limits to dispersion, promoting aggregation and increased polygyny (Campagna *et al.,* 1993; Baldi *et al.,* 1996). Therefore, in addition to using ENFA to compare grey seal habitat preferences at topographically dissimilar sites, there is ample scope for a similar exploration of the habitat preferences of other species both for interspecific comparisons and for intraspecific comparisons at multiple sites.

As outlined above, conspecific interactions are likely to play a major role in the distribution of individuals of any colonially breeding pinniped species; for example, one of the main causes of death in southern sea lion (*Otaria flavescens*) pups is aggression resulting in infanticide by subordinate males (Campagna *et al.,* 1992), though the mortality rate declines for pups of more gregarious females. However, this does not apply to all pinnipeds, as many ice-breeding phocids breed far from other individuals. This highlights the importance of carefully considering the breeding biology and general ecology of the focal species if extending the ENFA approach to other species, particularly when choosing additional predictor variables, which may not be relevant to the grey seal at North Rona. With the exception of scavenging gulls, terrestrial predation does not present a severe threat to grey seals at North Rona; however, pinnipeds elsewhere may be vulnerable to predation whilst hauled out to breed. For example, brown

hyaena, *Parahyaena brunnea*, predate upon breeding Cape fur seals along the Namibian coast, *Arctocephalus pusillus pusillus* (Wiesel, 2010) and the intensity, frequency and type of predation may influence the degree of aggregation within the breeding colony (Hirsch and Morrell, 2011). In addition, the degree of maternal attendance in species such as the Cape fur seal is dramatically different to that seen in the grey seal; the Cape fur seal, amongst the other income-breeding pinniped species, returns to the sea to feed (e.g. Oftedal *et al.,* 1987) or to cool off during the lactation period (e.g. Gentry, 1973; Campagna and Le Boeuf, 1988). Therefore, the importance of proximity to pools of water may not be apparent, and the pup-pool trade-off discussed above may not be as pertinent in these species, though a trade-off may exist between time spent in the sea, or in locomotion between the sea and the pup, and attending the pup. Also, in many pinnipeds, particularly the ice-breeding phocids (e.g. the Weddell seal, *Leptonychotes weddellii*, and harp seal, *Pagophilus groenlandicus*), the climate during the breeding season may not generate a need for behavioural thermoregulation, and more important 'resources' may include ice holes for predator avoidance or feeding (e.g. Kovacs *et al.,* 1996; Lydersen and Kovacs, 1999), or ice edges for access to open water (Stewart, 1987). Conversely, pools may still be important for drinking, as many other pinniped species have been shown to drink water whilst on land (Gentry, 1981), including freshwater drinking in the Antarctic fur seal (*Arctocephalus gazella*; Lea *et al.,* 2002), whilst ice-breeders may eat ice or snow to achieve the same benefit (SDT, *pers. comm.).*

6.3.3 Broader implications of female distribution on pinniped ecology

It has long been recognised that space availability is likely to be a key determinant of female distribution and aggregation (Emlen and Oring, 1977), and this is particularly true of dense breeding aggregations of pinnipeds such as the grey seal (Pomeroy *et al.,* 1994, 2000a) and the southern elephant seal (Baldi *et al.,* 1996). In turn, the distribution and aggregation of females affects the mating behaviour and reproductive success of both males and females by directly influencing mate access and mating opportunities (Bartholomew, 1970; Emlen and Oring, 1977; Boness and James, 1979; Stirling, 1975; Twiss *et al.,* 2007). Where females are highly aggregated, for example around specific habitat features such as pools of water, it is likely that individual dominant males will be able to monopolise access to groups of these females, or the resources themselves (Stirling, 1975; Le Boeuf, 1991; Cassini, 1999; Twiss *et al.,* 2007). Given the importance of pools of water in determining female distribution as shown in this study, amongst others (Twiss *et al.,* 2000, 2001, 2007; Redman *et al.,* 2001), it is therefore clear that the distribution of pools (as well as their salinity and proximity to access) will affect the ability of males to monopolise mating opportunities, thus directly influencing the degree of polygyny and sexual selection observed. Indeed, Twiss *et al.* (2007) have shown that during dry spells with few pools of surface water on North Rona, it is more difficult for dominant males to monopolise matings. It appears that this is because females spend considerable amounts of time in locomotion between pools

and their pup in drier conditions, allowing less dominant males to gain matings. Thus, simple changes in pool distribution brought about by local climatic variability can directly alter the annual proportion of males contributing to the effective population size by up to 61% (Twiss *et al.,* 2007). The intra- and inter-annual variability in pool distribution discovered in this study, through its effects on the environmental potential for polygamy, is therefore likely to have a large annual impact on the genetic structure of the population as well as the distribution and behaviour of males at North Rona, including the number and scale of aggressive interactions brought about by competition for mating opportunities (Twiss, 1991; Twiss *et al.,* 1998). This has broad implications for the majority of sexually reproducing animal taxa, since the distribution of females in most species will be determined by the resource distribution. Indeed, direct parallels may be observed in other pinnipeds, whose distributions (especially in temperate and tropical climates) are influenced by the availability of resources for thermoregulation (e.g. shade or pools of water; Boness, 1991; Le Boeuf, 1991; Wolf *et al.,* 2005). In addition to directly affecting male behaviour and mating success, female distribution may affect pup behaviour, as discussed in Section 6.4.3.

6.4 Future extensions of this research

6.4.1 A consideration of the potential drivers of decline at the North Rona colony

North Rona has experienced a substantial decline in the number of breeding seals (and therefore in annual pup production) over the last decade (Smout *et al.,* 2009; CDD and PPP, *unpubl. data*; Section 3.3.1). This decline is particularly strange given the overall growth experienced by other populations in the Outer Hebrides, and in the UK in general (Duck and Morris, 2011). Though it has previously been suggested that the size of a population may be limited by the availability of pupping sites of the required size and conditions (Harwood and Prime, 1978), this does not appear to be limiting the population or causing its decline at North Rona. The grey seal appears to be relatively tolerant of changes in its immediate environment (Chapter 4), and North Rona has previously supported much larger populations, suggesting that suitable pupping sites are currently in excess. In fact, the decline of the North Rona colony appears to be caused primarily by a decreasing rate of female return (PPP, *pers. comm.*), though in the following discussion the potential for high pup mortality will also be considered. This seems appropriate as first year survival is often an important parameter in the description of population dynamics; in a review of 160 studies of marine mammal and terrestrial herbivore population dynamics, Sinclair (1996) found first year survival to be the most important parameter in 36% of cases. Predation on breeding grey seals is rare and infrequent at North Rona as its remote, offshore location excludes typical terrestrial predators of pinnipeds such as bears (Hammill and Smith, 1991) and humans (Lambert, 2002) or canids (Culloch *et al.*, 2012; Wiesel, 2010). Predation events are typically due to greater black-backed gulls targeting young and vulnerable pups,

especially those that have been temporarily or permanently abandoned by their mothers (PPP and SDT *pers. comm.;* Twiss *et al.,* 2003). Even where these gulls do not attack the pup directly, their activity near the mother-pup pair whilst scavenging for the placenta immediately after parturition (Figure 6.1) may affect the formation of the mother-pup bond and lead to abandonment, which would lead rapidly to pup death from starvation or trampling (Baker, 1984, 1988; Baker and Baker, 1988; PPP, *pers. comm.*). Indeed, failure of mother-pup bond formation was found to precede half of all pre-weaning pup deaths at two UK breeding colonies (Anderson *et al.,* 1979). This is likely more common on the periphery of the colony, potentially due to the lower densities of seals in these areas (Redman *et al.,* 2001; Twiss *et al.,* 2003). Fine scale site topography has been shown, here and elsewhere, to influence female distribution; a pattern of topography that leads to greater dispersion in some areas, or increased mother-pup distances (such as limited pool availability in dry years, Twiss *et al.,* 2007) could, therefore, reasonably have a tangible influence on the degree of predation experienced within a breeding season, though Twiss *et al.* (2003) found no link between local adult female density and the likelihood of pup death. However, in a declining population such as that at North Rona, it may be that a threshold in adult density may be reached that allows more gulls to get in amongst the female and pup groupings. Section 3.3.3 showed that overall, in the later seasons considered (e.g. 2010), there are more females at large distances from their nearest neighbour than in the earlier seasons (e.g. 1998) (Figure 3.10), suggesting that this may already be occurring. Increased pup mortality could also reasonably be caused by a reduction in average maternal bodily condition, which could cause insufficient provisioning of the pups which, after weaning, may fail to hunt successfully before starvation sets in (Hall *et al.,* 2001). This could be tested by assessing recent changes in average maternal mass and maternal mass transfer to the pup, building on the work of Pomeroy *et al.* (2001). If present, this decline in maternal bodily condition would likely be caused by declining fish stocks in key foraging areas. However, changes in maternal mass would only be detected if all seals are similarly affected; if females in poor condition show lower rates of return (for example due to starvation) or abortion of the foetus, but females in good condition do not, then no decline in observed maternal mass, mass transfer or observable impacts on the pup would be expected.

Figure 6.1: Black-backed gulls scavenging for a placenta shortly after a grey seal birth in the SS on North Rona. Photograph by PPP (2010).

The potential for a decline in food availability is interesting as it may lead to reduced rates of recruitment and female return due to starvation of juveniles and adult females between breeding seasons. To address this it is important to discover where grey seals typically forage. This is an area of pinniped ecology that is largely understudied, mainly due to the difficulty and expense of performing large scale Global Positioning System (GPS) or Satellite Relay Data Logger (SRDL) tagging operations to assess individual movement patterns in the marine environment (e.g. McConnell *et al.,* 1999; Matthiopoulos *et al.,* 2004; Section 6.4.4). Although fish stocks in the Atlantic and the North Sea are known to have drastically declined in recent years (ICES, 2006, 2011; Edwards, 2011) it is not apparent why this might cause the decline of the North Rona seal population whilst other nearby populations expand. However, some of the prey species found to be most important in the diet of grey seals around the Hebrides (cod (*Gadus morhua*), ling (*Molva molva*) and whiting (*Merlangius merlangus*); Harris, 2007) are also those that have shown some of the sharpest declines (Edwards, 2011). This further emphasises the need to perform tracking studies to assess foraging areas of seals both from North Rona and from nearby colonies.

Tracking studies may also identify whether North Rona seals forage in areas known to be affected by Amnesiac Shellfish Poison (ASP) toxicity, and assessments of the toxin load of individual seals using faecal and urinary analysis from deposits on the breeding colony could supplement the tracking studies, as this is the most useful method for monitoring ASP presence (Lefebvre *et al.,* 1999; Hall and Frame, 2010). ASPs accumulate in shellfish following their synthesis in phytoplankton such as the diatom *Pseudo-nitzschia spp.,* which are a common part of the Scottish phytoplankton community (Fehling *et al.,* 2004; 2006; Fraser *et al.,* 2004). *Pseudo-nitzschia spp*. can synthesise the ASP domoic acid, a neurotoxin known to have effected large-scale marine mammal mortality (Gulland and Hall, 2007). Following acute exposure to high concentrations of domoic acid, California sea lions strand whilst experiencing seizures, ataxia and occasionally coma before death (Gulland *et al.,* 2002). A number of effects of lower level chronic toxicity have also become apparent, including neuronal loss and hippocampal atrophy (Goldstein *et al.,* 2008) which result in individuals stranding and frequently re-stranding, developing epilepsy and/or abnormal aggressive behaviour and travelling far outside of their 'normal' ranges. Shellfish containing such toxins form part of the typical grey seal diet (Bowen *et al.,* 1993; Bowen and Harrison, 1994; Hammond *et al.,* 1994; Thompson *et al.,* 1996; Mikkelsen *et al.,* 2002) and can take years to detoxify, even when causative phytoplanktons are no longer present (Stobo *et al.,* 2008). This could potentially influence female site fidelity and natal colony return by disrupting neural activity and navigation; though it may be expected that all local colonies would be similarly affected. That only a subset of colonies could be affected may result from differing diets between colonies, which were shown by distinct blubber fatty acid profiles between the North Rona and Isle of May colonies (Walton *et al.,* 2000). This may also help to explain why males are

disappearing from North Rona disproportionately quickly relative to females (SDT, *pers. comm.*). Males, being of a generally larger size, are likely to consume more food and may therefore ingest more ASPs. Individuals of a larger body size for their sex would also, therefore, be expected to be declining disproportionately rapidly relative to smaller conspecifics of the same sex. There may also be sex differences in foraging strategies, which could contribute to this apparent difference: adult males from the western North Atlantic stock at Sable Island tend to feed on more benthic prey, whilst pelagic prey are targeted by females and juveniles (Tucker *et al.,* 2007), consistent with known dive and foraging patterns in the Sable Island population (Beck *et al.,* 2003).

Interestingly, there is already some evidence of domoic acid exposure in Scottish harbour seals, which has been identified as a potential factor in their decline (Hall and Frame, 2010). Although this clearly represents a very coarse assessment of the possibility of ASP toxicity in grey seals, areas identified as potential grey seal foraging areas (Matthiopoulos *et al.,* 2004) are also areas that have been assessed as showing high concentrations of ASP toxins in local shellfish populations (Stobo *et al.,* 2008; Figure 6.2). Perinatal exposure of the pup to ASPs is also possible: toxins accumulate in the amniotic fluid, often leading to abortion (Brodie *et al.,* 2006). Furthermore, it has been observed that domoic acid may be passed on between rats in their milk (Maucher and Ramsdell, 2005). Given the high transfer of milk in the short lactation period of grey seals, such an occurrence in grey seals could also negatively affect pup health and navigation abilities. Further studies are also needed to determine the impact of other sources of mortality in grey seal populations, such as shipping (Bexton *et al.,* 2012) and illegal killing (SCOS, 2011).

An alternative explanation for the declining rate of female return is that they are simply pupping at different colonies. There is some evidence of inter-colony translocations in grey seals from North Rona (Harwood *et al.,* 1975; Pomeroy *et al.,* 1994, 2000; SDT, *pers. comm.*). Some of these translocations occur locally (e.g. 150km from North Rona to Orkney, Pomeroy *et al.,* 1994), whilst some pups have been resighted in Norway, the Faroe Islands and western Ireland shortly after weaning, with few data on returns to their natal sites following such long distance translocations (Hewer, 1974). However, these studies are based on relatively old data from a time when the colony was larger and more stable (Hiby *et al.,* 1996; Pomeroy *et al.,* 2000), so it would be interesting to re-examine the evidence for translocations in light of the recent colony decline. Matthiopoulos *et al.* (2005) stressed the importance of considering density-dependent effects at two distinct spatial scales: local (colony-wide, within a study site; e.g. availability of pupping sites) and global (outwith the study site, e.g. food availability). In light of recent research, including that presented here, it appears relatively unlikely that density-dependent effects at a local scale could be directly causing the decline of the North Rona colony. It is therefore vital that further research is carried out to consider the 'global' drivers of decline, as outlined above.

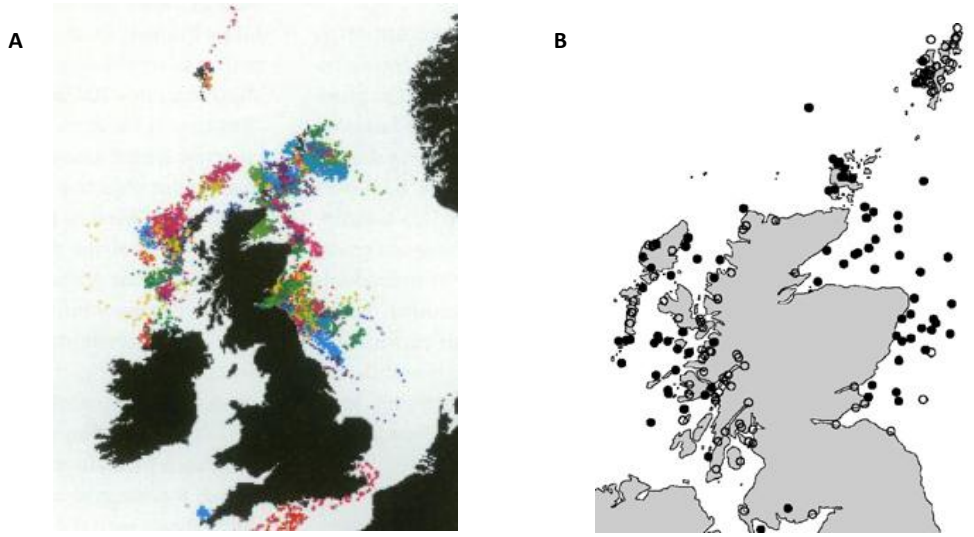

Figure 6.2: Comparison of **A:** foraging areas of grey seals, where different colours represent foraging areas of different colonies (from Matthiopoulos *et al.,* 2004) and **B:** areas known to be affected by ASP toxicity, where filled circles indicate sites where ASP toxins were found in shellfish samples, using high-performance liquid chromatography (from Stobo *et al.,* 2008).

Photo-identification studies (e.g. Vincent *et al.,* 2001; Karlsson *et al.,* 2005; Hiby *et al.,* 2012) to identify individual females could be used effectively to build a digital database of known females in Britain. This database could be used alongside a mark-recapture model to provide a relatively inexpensive, hands-off method of identification and tracking to assess individual movements between haul-out and breeding sites. Such a database could thus be an important resource in tracking individuals and informing studies of population dynamics. Furthermore, the individuality and temporal stability of the pelage markings used to identify individuals (Ridoux *et al.,* 2001) has additional benefits in that they are more reliable than flipper tags, which are lost from adult females at an estimated rate of 0.24 annually, though likely at a higher rate from juveniles (PPP, *unpubl. data*) and can be difficult to read, especially from a distance. The range of potential alternative haul-out and breeding sites over a wide geographic area make this a particularly difficult and long-term endeavour, though considerable progress is being made and automation of the photo-ID process will speed this further (e.g. Hiby *et al.,* 2012).Further research into the cause of decline should therefore focus on causes of mortality and poor inter-annual return rates.

6.4.2 Assessment of disturbance effects

6.4.2.1 Abiotic disturbance

As a result of the remote nature of the island, grey seals at North Rona typically experience minimal disturbance throughout the breeding season. Disturbance generally occurs as a result of conspecifics and scavenging gulls (e.g. Twiss *et al.,* 2003), with minimal disturbance from researchers, who plan their activities within the colony to minimise significant disturbance as much as possible (Pomeroy *et al.,* 2000). As the seals generally breed inland, away from the

access points, tidal effects do not represent a problem at North Rona. However tide may play an important part in the distribution of seals at beach-based colonies such as Donna Nook. Indeed, in the 2011 breeding season, a high spring tide event caused large high density aggregations of grey seals to form along a small section of the beach not inundated by sea water (A.M. Bishop, *pers. comm.*). Likewise, the distribution of southern elephant seals was found to be influenced by normal tidal patterns; for example, a group of 85 females occupied an area of 1000m^2 at high tide, but 4000m^2 at low tide (Baldi *et al.,* 1996). Furthermore, grey seal pups at Ramsey (Wales; 51°52'N 5°21'W) were found to experience greater mortality than at sites such as Auskerry (Scotland; 59°2'N 2°34'W) during periods of high breeding density caused by high tide events (Anderson *et al.,* 1979). This may be worth considering in the long term as sea levels are expected to rise over the next century (Jenkins *et al.,* 2009), and sea level rise has already been suggested to influence pinniped haul-out behaviour (Funayama *et al.,* 2012). Grey seals (and other pinnipeds) breeding on ice are typically found at lower densities than on land, and choose ice-based sites over land-based sites where these are available (Jüssi *et al.,* 2008). The extent of ice coverage will therefore influence the breeding density and distribution of seals in, for example, the Baltic Sea (Jüssi *et al.,* 2008), though may have consequences for a range of ice-breeding pinnipeds worldwide. This is likely to be influenced by future climate change and should be considered in any predictive models for such species and areas. In addition to this natural disturbance, seals at other sites may experience anthropogenic disturbance.

6.4.2.2 Anthropogenic disturbance

The ecotourism industry, including wildlife watching (Giannecchini, 1993), is expanding both nationally and globally, often providing multiple local benefits including supplementary income, education and leisure opportunities (Brock, 1994). These opportunities are readily exploited at the expanding and easily accessible Donna Nook grey seal breeding colony, which forms annually between late October and December: the Lincolnshire Wildlife Trust (LWT) provides educational information to the thousands of ecotourists visiting the site. The LWT also provides a warden service to protect the breeding seals, as tourists are capable of attaining close proximity to both mothers and pups throughout the season (Figure 6.3). Balmford *et al.* (2002) and others (e.g. Nabhan and Trimble, 1994; Louv, 2006) link a loss of knowledge about the natural world to growing isolation from it, and suggest the importance of re-establishing links with nature to avoid declines in support for biodiversity conservation. In an age where UK primary school children can correctly identify more 'Pokémon' species (synthetic characters in the trading-card and video game series developed by Satoshi Tajiri; Tobin, 2003) than types of common UK wildlife (Balmford *et al.,* 2002), the education opportunities at such a site are clearly very valuable. Despite the distinct educational benefits of such close proximity to wild nature, this may also represent a major form of disturbance to the seals.

Human contact and disturbance have previously been shown to impact upon animal behaviour and space use (Olson *et al.,* 1997; Anthony and Blumstein, 2000; Lacy and Martins, 2003; Végvári *et al.,* 2011). Though some animals may habituate to human presence and activities (e.g. Romero and Wikelski, 2002; Lacy and Martins, 2003), individuals of particular 'behavioural types' may not do so (Ellenberg *et al.,* 2009). Many of the seals at Donna Nook are found very close to the fence at which tourists gather (Figure 6.3; *pers. obs.*); it is possible that these individuals habituate more readily to disturbance, whilst those that remain sensitive to disturbance may represent an alternative 'behavioural type' that choose sites further away to avoid human contact. This raises interesting questions about the influence of disturbance on the distribution patterns within the colony. Martin and Réale (2008) have shown, for example, that Eastern chipmunk (*Tamius striatus*) distribution is affected by disturbance: individuals with more docile and exploratory 'temperaments' are found more often in areas frequented by humans. Furthermore, traits such as docility are known to be heritable (Dingemanse *et al.,* 2002). This suggests a potential mechanism for natal philopatry and hints towards the possibility of local kin associations forming as a result of individuals of similar inherited temperaments avoiding or habituating to local disturbance, with a positive feedback effect of 'docile' (habituated) and philopatric individuals mating with similarly docile and philopatric individuals (assuming that the same mechanisms of philopatry and habituation are involved for both males and females).

Figure 6.3: Demonstration of the close proximity of tourists to breeding seals at Donna Nook. Photograph by J.P.A. Carter (Carter, 2007).

Aside from the potential for disturbance effects on individual distribution patterns, disturbance is known to induce stress and increased energy expenditure in many wild animals (e.g. Dyck and Baydack, 2004; Ellenberg *et al.,* 2006, 2007, 2009). A stress response in seals affected by disturbance could induce behavioural changes that impact upon a mother's activity budget or reduce the energy available for pup provisioning, with implications for reproductive success (Ellenberg *et al.,* 2007). For example, an increased rate of pup checking and alert behaviours in response to disturbance could result in poor pup condition at weaning as a result of

reduced nursing behaviour. Twiss *et al.* (2012) demonstrated that individuals with different 'behavioural types' (proactive *versus* reactive) show different responses to disturbance in terms of pup checking behaviour. If this carries across to the effects of anthropogenic disturbance at sites such as Donna Nook then anthropogenic disturbance may be expected to influence different behavioural types in different ways, with implications for the genetic and behavioural type structure of the local population. Given the potential for disturbance influencing the distribution of these behavioural types, it may also be that differential reproductive success could be experienced depending on location; it is important that future research is rigorous in teasing this apart from the effects of topography and water availability on reproductive success. The implications of 'personality' and 'behavioural types' will be discussed further in Section 6.4.3. Disturbance could be included in an ENFA as an 'EGV' layer, using a 'cost-distance' approach (similar to CFEM in Chapter 5), but weighted to indicate the intensity or presumed effect of the disturbance, for example weighted by number of people present, noise level, duration of disturbance or proportion of time spent disturbed.

6.4.3 Consistent Individual Differences

Chapter 4 dealt with population responses to a changing environment within and between multiple breeding seasons, whilst chapter 5 dealt with intraspecific variation in site use. However, there is also important variation *within* sex/age classes not captured by these approaches, i.e. individual variation in preferences. Though individual females will likely differ in their choices, for example through the effects of condition on requirements for pools for thermoregulation, it is possible that individual females may be consistent in their preferences within and between seasons, and may react to changing conditions in a consistent manner. This consistency may be based on any of the relevant environmental predictors of site choice, CACC, CPOOL, salinity or biotic variables such as distance to nearest female, or their pup, or even habitat suitability. Pomeroy *et al.* (2005) found that females at North Rona returned to within a median distance of 39m of the previous year's pupping site, though this investigation was based on geographic location alone, and site fidelity was not assessed with regards to individual fidelity to particular habitat attributes. However, an analysis of CIDs in site choice might highlight individual fidelity to a particular range of ecogeographical features and may therefore provide greater depth to our understanding of geographical site fidelity. It would be particularly interesting to assess whether females that translocate to different colonies between years (Hewer, 1974) tend to choose sites with similar ecogeographical features at geographically separate sites.

Intraspecific variation in site preferences could also be important to consider with regards to individual tolerance of environmental change. The ENFA indicated that female grey seals show a high degree of tolerance in their on-land habitat and pupping site preferences (i.e. they occupy

a relatively wide, though restricted, range of conditions) and are therefore likely to be able to adapt to local changes. However, this is a population-based approach and the same may not be true for individual females, which may be highly specialised and intolerant of change (Figure 6.4A). As highlighted by Bolnick *et al.* (2003), treating conspecifics as ecologically equivalent is only appropriate if individual niche variation has a trivial effect on ecological processes or is rare or weak (Figure 6.4B). In this case, the within-individual component (WIC; the average variance of individual resource use, essentially equivalent to the ENFA-computed specialisation value) will make up a large proportion of the species total niche width (TNW). However, where the between-individual component (BIC) of the variation in resource use is large, and the WIC makes up a small proportion of the TNW (Figure 6.4B), each individual may be highly specialised in their resource use. An investigation of individual consistency would indicate whether the adaptability suggested by the low specialisation values is a property of the individual or the population. Few studies have attempted to quantify this inter-individual variation relative to the population variability. However, in many cases this variation comprises the majority of the population's TNW and such individual specialisation in resource use appears to be widespread (Bolnick *et al.,* 2003).

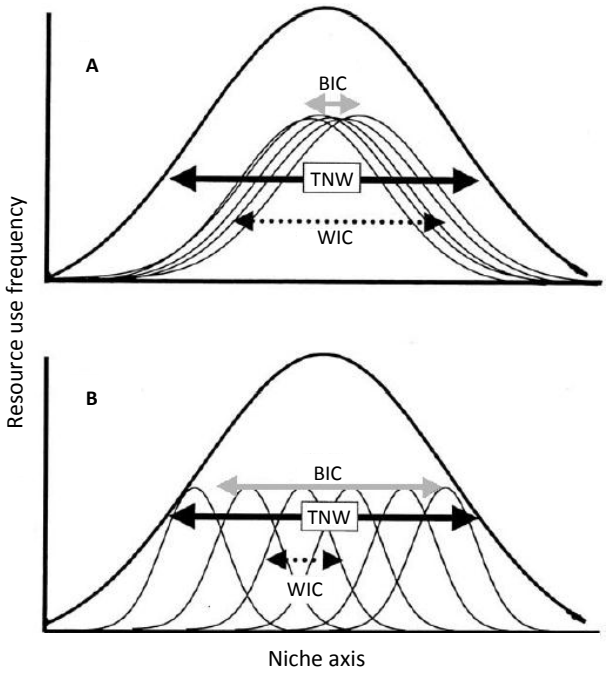

Figure 6.4: Schematic diagram of the population niche (thick curve) subdivided by individual resource use. The total niche width (TNW; black arrow) is the variance of total resource use across the population. TNW = WIC + BIC, where WIC (dotted arrow) is the average of individual niche widths and is equivalent to individual niche width, whilst BIC (grey arrow) is the variance in mean resource use between individuals. Although the Gaussian curves used here are generally a poor description of a real niche, they usefully convey the concept of between-individual variation. Figure **A** exemplifies a population of generalist individuals, where WIC represents a large proportion of TNW; Figure **B** depicts a population of specialised individuals, where TNW is composed of greater BIC and the WIC is small. *Adapted from Bolnick et al. (2003).*

Consistent individuals differences (CIDs) in behaviour have been the subject of increasing research over the past two decades, with various terms being proposed to describe them,

including animal 'personality' (Stamps and Groothuis, 2010), coping styles (Koolhaas *et al.,* 1999), temperament (Réale *et al.,* 2007) and behavioural syndromes (Sih *et al.,* 2004). Regardless of the terminology, these CIDs have been identified in an increasingly wide range of taxa, including birds (e.g. Quinn and Cresswell, 2005), fish (e.g. Magnhagen and Bunnefeld, 2009), arthropods (e.g. Johnson and Sih, 2007), cnidarians (e.g. Briffa and Greenaway, 2011) and mammals (e.g. Réale *et al.,* 2000), including grey seals (Twiss and Franklin, 2010; Twiss *et al.,* 2011, 2012*;* Culloch*,* 2012). These studies of grey seal CIDs represent some of the few that have been performed *in situ* rather than in captivity, though knowledge of how CIDs interact with environmental factors to shape individual fitness is key to understanding their ecological relevance. It would be interesting to investigate responses to the pup-pool trade-off and establish whether they are consistent within females, either between or within breeding seasons. The response to any trade-offs, for example between proximity to pool and to pup, will likely vary between individuals (McNamara and Houston, 1996), though it is possible that individual females will react consistently to changing conditions (Twiss *et al.,* 2012). Twiss *et al.* (2012) have identified a pro-active/re-active axis in grey seals similar to that discovered in a range of taxa, predominantly in birds (chickens, van Hierden *et al.,* 2002; great tits, Carere *et al.,* 2005) and mammals (laboratory rodents, Koolhaas *et al.,* 2001; mink, Malmkvist and Hansen, 2002; pigs, Hessing *et al.,* 1993). CIDs, including classifications of pro-/re-activity, may apply over various contexts. For example, 'proactive' individuals are often described as aggressive, bold and inflexible, with these traits coming across in mating, social and foraging contexts (e.g. Benus *et al.,* 1992; Koolhaas *et al.,* 1999; Carere *et al.,* 2010). These classes of individuals likely lie along a continuum of 'behavioural types' (Twiss *et al.,* 2012), and individual strategies are thought to represent alternative adaptive strategies (Koolhaas *et al.,* 1999), which are heritable (Dingemanse *et al.,* 2002; van Oers *et al.,* 2003). The pro-/re-active axis has been linked to the propensity for an individual to explore (Carere *et al.,* 2005), with proactive individuals typically being known as 'fast' explorers that settle easily into routines and may therefore be less responsive to a changing environment than reactive individuals, which explore the environment carefully and respond cautiously (Sih *et al.,* 2004). On the other hand, proactive individuals may out-compete reactive individuals in a stable environment, investing less energy in unnecessary investigations of, and responses to, the environment (Koolhaas *et al.* 1999). As the fine-scale distribution of pools is so variable on North Rona within and between years it would be interesting to investigate the responses of individuals to changing climates, whether some are restricted by their 'personalities', and whether these responses have any measurable effects on fitness.

Given the common stability of behavioural types across contexts (i.e. between ecologically dissimilar processes or behaviours such as feeding and mating behaviours; Johnson, 2001; Johnson and Sih, 2007) it would also be interesting to establish whether the behavioural

types assigned to females in terms of pup checking behaviour by Twiss *et al.* (2012) carry over to contexts such as site selection and exploratory behaviour, for example in the face of climatic variability. Indeed, recent work by Boon *et al.* (2008) demonstrates that personality, measured in terms of pro-/re-activity, can affect habitat use and movement (of North American red squirrels, *Tamiasciurus hudsonicus*), demonstrating that personality may have fitness consequences based on variability in habitat quality. Furthermore, as highlighted above, individuals may demonstrate consistency in site preferences, and it would be interesting to investigate how this corresponds to other metrics of an individual's behavioural type. Indeed, 'proactivity' in an individual is often associated with increased aggressiveness relative to that expressed by reactive individuals (Koolhaas *et al.,* 1999, 2010). If proactive female grey seals (Twiss *et al.,* 2012), also tend to be more aggressive it is possible that they may be better able to access and monopolise their preferred, higher quality sites around pools of water that tend to attract higher female densities (Twiss *et al.,* 2012). Twiss *et al.* (2012) found that proactive females did, in fact, tend to engage in more aggressive interactions with female conspecifics, though it is important to note that this may be an effect of them being found more often in high density areas in closer proximity to their nearest neighbours, making inference regarding causality difficult.

Finally, there is growing evidence that individual behaviour can be greatly influenced by social and environmental factors experienced early in life (e.g. Stamps, 2003; Stamps and Groothuis, 2010; Trillmich and Hudson, 2011); this provides a potential direct link between pupping site (which influences female behaviour; Redman *et al.,* 2001) and pup social and behavioural development. For example, guinea pig (*Cavia aperea* f. *porcellus*) pups tend to be more exploratory if they have spent long periods of time separated from their mother (Albers *et al.,* 2000). This is an intriguing relationship, and it would be interesting to investigate whether female grey seals with pupping sites far from pools (that spend a large proportion of their time in locomotion between a pool and their pup) tend to have more exploratory pups, and whether these exploratory tendencies are maintained across development and represent a 'behavioural type' that is expressed in other contexts, such as foraging.

6.4.4 Seals at sea

Due to the focus on grey seal habitat use during the breeding season, this research has not considered the marine habitat preferences of grey seals. As marine mammals, pinnipeds in general spend a lot of time in the water and little is known about UK grey seal habitat use or preferences in this time (Harvey *et al.,* 2012), especially with regards to the seals breeding at North Rona. This is an interesting area for future research, which should explore seal distribution in relation to prey abundance and bathymetric and oceanographic features including proximity to haul out sites (e.g. Harvey *et al.,* 2012). Summer re-sights on North Rona suggest that the island is

also used as a summer haul out by at least one third of the females that breed there during the autumn (Pomeroy *et al.,* 2005), though the remainder are unaccounted for. The use of alternative haul-out sites and the factors driving this would also be interesting to investigate. As outlined in Section 6.4.1, this could have drastic implications for the health of the North Rona colony as where the seals feed will influence their exposure to pathogens (Härkönen *et al.,* 2006), ASPs (such as domoic acid; Stobo *et al.,* 2008; Hall and Frame, 2010), fisheries (e.g. Harding *et al.,* 2007; Bäcklin *et al.,* 2011) and shipping interactions (Bexton *et al.,* 2012) and their likelihood of behavioural alterations as a result of interactions with renewable energies developments (e.g. Edrén *et al.,* 2010; Skeate *et al.,* 2012). Tracking studies would be very useful in addressing these questions. Although an entirely hands-off photo-ID approach would be useful in tracking movements between haul-outs (e.g. Karlsson *et al.,* 2005; Hiby *et al.,* 2012) this would require unfeasible amounts of time to monitor a sufficient proportion of possible sites and would provide only a very coarse indication of foraging areas. Therefore, satellite tagging approaches (e.g. McConnell *et al.,* 1999; Matthiopoulos *et al.,* 2004; Harvey *et al.,* 2012) would be more useful, though would have to target a large proportion of the population in order to provide an effective measure of grey seal site use. Chapter 5 proposed the possibility of resource-use segregation between conspecific age classes; this could be expanded when performing tracking studies of grey seals at sea to determine whether separate sex or age classes forage in distinct areas or on distinct prey, and could confirm whether, for example, weaners that associate on land during the PWF also associate at sea during foraging trips.

It would also be interesting to explore whether the 'personalities' outlined in Section 6.4.3 are also expressed in behaviours at sea. For example, bold, exploratory individuals might gain a fitness benefit by being better able to locate and monopolise food resources, attaining greater annual growth and possibly producing heavier pups at weaning in the next season. Although a fitness benefit may be expected, bolder individuals may suffer greater mortality from one-off events (as opposed to chronic causes of mortality such as disease and starvation), including incidental by-catch (e.g. Harding *et al.,* 2007; Bäcklin *et al.,* 2011) or shipping collisions (Bexton *et al.,* 2012) as a result of hazardous foraging behaviours. In order to examine consistent individual differences in behaviour individuals must be tracked within the breeding season, which can be achieved as a result of the individual pelage markings of males and females. To assess behavioural consistency over a longer period, and investigate potential long-term fitness consequences of these behaviours, long-term longitudinal studies of the same (identified) individuals are important. The importance of longitudinal datasets has been recognised previously (e.g. Nussey *et al.,* 2005; Moyes *et al.,* 2009); such a dataset exists for many of the individuals at North Rona, which represents an excellent resource for a study of this nature.

6.5 Final conclusions

In conclusion, this research has satisfied the main aims set out in Section 1.5, elucidating the pupping site and habitat preferences of adult females, and the space use preference of weaned pups relative to neonates over multiple seasons, with some inter- and intra-seasonal variability. This has confirmed previous ideas regarding important habitat features and identified the importance of pool salinity to female distribution, confirming that seals drink from pools of 'fresh' water at North Rona. However, aerial photographs of the North Rona colony are available for the last two decades, and there is also a considerable archive of photographs for all of the major Scottish colonies; therefore there is ample opportunity for a temporal and spatial expansion of this study which could shed further light on grey seal site preferences. In relation to the North Rona population specifically, many of the females for which location data are available have also been individually identified by their stable pelage patterns in an extensive photo-ID effort; these individuals can therefore be associated with the EGV and HS values at their pupping sites and subsequent habitat, and thus tested for intra- and inter-seasonal consistency, contributing to our understanding of grey seal site fidelity, and the ongoing exploration of grey seal 'personality'. Furthermore, there is a substantial amount of fitness and reproductive success data available for these individuals; this represents an excellent opportunity to identify the fitness consequences of female pupping site and habitat choice, and alternative solutions to the pup-pool trade-off identified in this thesis.

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Appendices

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Appendix 1

Table A1.1: Critical values of the nearest-neighbour index, *R* (one-tailed). From Ebdon (1985: 220).

	Significance level					Significance level			
n	**0.05**	**0.01**	**0.005**	**0.001**	**n**	**0.05**	**0.01**	**0.005**	**0.001**
2	0.392	0.140	0.048	-	**34**	0.853	0.791	0.769	0.724
3	0.504	0.298	0.223	0.071	**35**	0.855	0.794	0.773	0.728
4	0.570	0.392	0.327	0.195	**36**	0.857	0.797	0.776	0.732
5	0.616	0.456	0.398	0.280	**37**	0.859	0.800	0.779	0.735
6	0.649	0.504	0.451	0.343	**38**	0.861	0.803	0.782	0.739
7	0.675	0.540	0.491	0.392	**39**	0.862	0.805	0.785	0.742
8	0.696	0.570	0.524	0.431	**40**	0.864	0.808	0.787	0.746
9	0.713	0.595	0.551	0.463	**41**	0.866	0.810	0.790	0.749
10	0.728	0.615	0.574	0.491	**42**	0.867	0.812	0.792	0.752
11	0.741	0.633	0.594	0.515	**43**	0.869	0.815	0.795	0.755
12	0.752	0.649	0.612	0.535	**44**	0.870	0.817	0.797	0.757
13	0.762	0.663	0.627	0.554	**45**	0.872	0.819	0.799	0.760
14	0.770	0.675	0.640	0.570	**46**	0.873	0.821	0.802	0.763
15	0.778	0.686	0.653	0.584	**47**	0.875	0.823	0.804	0.765
16	0.785	0.696	0.664	0.598	**48**	0.876	0.825	0.806	0.768
17	0.792	0.705	0.674	0.610	**49**	0.877	0.826	0.808	0.770
18	0.797	0.713	0.683	0.621	**50**	0.878	0.828	0.810	0.772
19	0.803	0.721	0.691	0.631	**55**	0.884	0.836	0.819	0.783
20	0.808	0.728	0.699	0.640	**60**	0.889	0.843	0.826	0.792
21	0.812	0.735	0.706	0.649	**65**	0.893	0.849	0.833	0.800
22	0.817	0.741	0.713	0.657	**70**	0.897	0.855	0.839	0.808
23	0.821	0.746	0.719	0.664	**75**	0.901	0.860	0.845	0.814
24	0.825	0.752	0.725	0.671	**80**	0.904	0.864	0.850	0.820
25	0.828	0.757	0.731	0.678	**85**	0.907	0.868	0.854	0.825
26	0.831	0.762	0.736	0.684	**90**	0.909	0.872	0.858	0.830
27	0.835	0.766	0.741	0.690	**95**	0.912	0.875	0.862	0.835
28	0.838	0.770	0.746	0.696	**100**	0.914	0.878	0.865	0.839
29	0.840	0.774	0.750	0.701	**200**	0.939	0.914	0.905	0.886
30	0.843	0.778	0.754	0.706	**300**	0.950	0.930	0.922	0.907
31	0.846	0.782	0.758	0.711	**400**	0.957	0.939	0.933	0.920
32	0.848	0.785	0.762	0.715	**500**	0.962	0.946	0.940	0.928
33	0.850	0.788	0.766	0.720					

Table A1.2: Critical values of a standard normal deviate z; used for checking the significance of the test statistic *c* in nearest neighbour analysis (Sections 3.2 and 3.3.2). From Ebdon (1985: 219).

	Significance level (one-tailed)			
	0.05	0.01	0.005	0.001
z	1.645	2.326	2.576	3.090
-z	-1.645	-2.326	-2.576	-3.090

Appendix 2: Appendix to Chapter 3

A2.1 Description of available habitat

The following four boxplots present the same data as is shown in Figures 3.1-3.4, inclusive of 'outliers'.

A2.1.1 Elevation

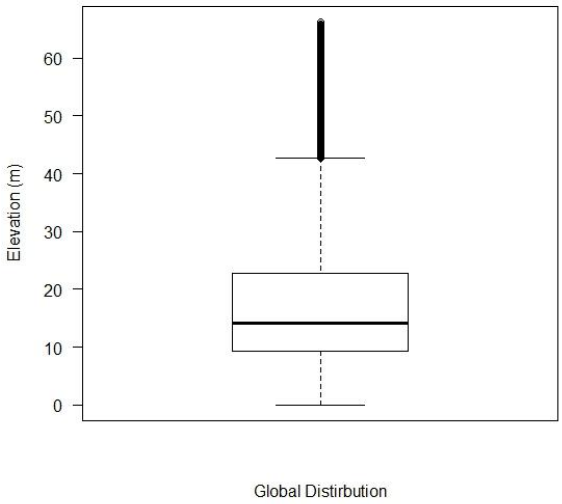


Figure A2.1: Global distribution of ELEV (m) across the study site. The whiskers show the value farthest from the median that is within 1.5IQR (inter-quartile range) of the upper and lower quartiles.

A2.1.2 Cost-distance to access

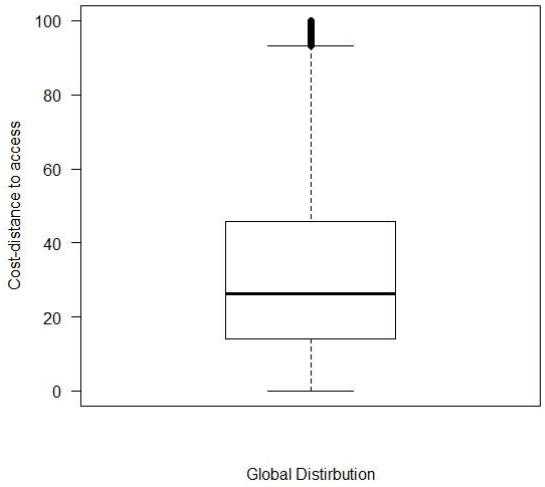


Figure A2.2: Global distribution of CACC values across the study site. The whiskers show the value farthest from the median that is within 1.5IQR (inter-quartile range) of the upper and lower quartiles.

A2.1.3 Cost-distance to pool

The MULTCOMP analyses on natural logarithm transformed data show that for every season the global CPOOL distribution changes significantly between stages (Figure A2.3; **1998:** $F_{2,246666}$= 2995, $p < 0.001$**; 2004:** $F_{2,246666}$= 890.5, $p < 0.001$**; 2008:** $F_{2,246666}$= 1857, $p < 0.001$**; 2009:** $F_{2,246666}$= 4040, $p < 0.001$**; 2010:** $F_{3,328888}$= 4539, $p < 0.001$). Post-hoc multiple comparisons demonstrate that the CPOOL changes between every stage of each breeding season, as shown in Figure 3.3, are statistically significant; the only exception to this was early-mid 2008, which showed no significant change (Table A2.1).

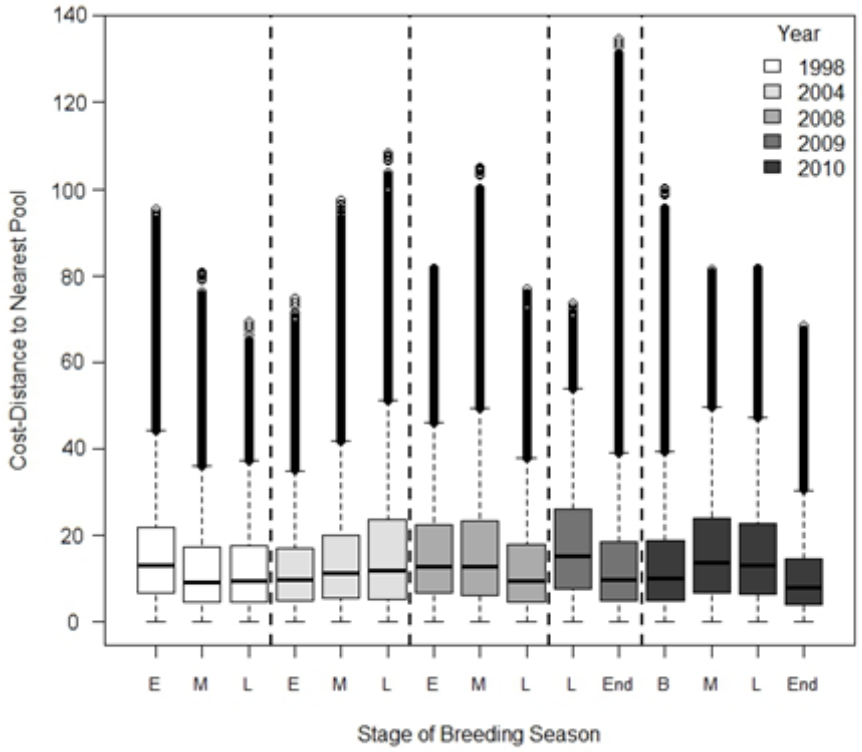


Figure A2.3: Global distribution of SAL values (‰) across the study site for all seasons. 'B': Beginning; 'E': Early; 'M': Mid; 'L': Late. The horizontal dashed line indicates the SAL median for all stages analysed; whiskers show the value farthest from the median that is within 1.5IQR (inter-quartile range) of the upper and lower quartiles respectively.

Table A2.1: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in CPOOL; *n* for each stage = 82223.

Comparison	t-value	*p*
1998early-1998mid	70.50	< 0.001
1998early-1998late	64.43	< 0.001
1998mid-1998late	-4.71	< 0.001
2004 early -2004 mid	28.32	< 0.001
2004early -2004late	-41.59	< 0.001
2004mid -2004late	-13.71	< 0.001
2008early-2008mid	0.876	0.655
2008early-2008late	53.77	< 0.001
2008mid-2008late	51.25	< 0.001
2009late-2009end	63.56	< 0.001
2010beginning-2010mid	-50.58	< 0.001
2010beginning-2010late	-42.09	< 0.001
2010beginning-2010end	52.31	< 0.001
2010mid-2010late	8.473	< 0.001
2010mid-2010end	105.42	< 0.001
2010late-2010end	96.47	< 0.001

A2.1.4 Salinity

MULTCOMP analyses on transformed data indicated that the global SAL distribution changes significantly between stages within each breeding season (Figure A2.4 **1998:** $F_{2,246666}$= 192.7, $p < 0.001$**; 2004:** $F_{2,246666}$=192.7, $p < 0.001$**; 2008:** $F_{2,246666}$= 192.7, $p < 0.001$**; 2009:** $F_{2,246666}$= 0, $p = 1$**; 2010:** $F_{3,328888}$= 7607, $p < 0.001$). Post-hoc multiple comparisons demonstrate that increases in SAL between each breeding season stage (as shown in Figures 3.4 and A2.4) were significant in nearly all cases (Table A2.2). The late and end stages of both 2009 and 2010 did not differ as the

salinity surfaces used for these stages were identical due to limited data availability (Section 2.4.3.3); the same trend is seen throughout 1998, 2004 and 2008 as they use the same set of SAL surfaces.

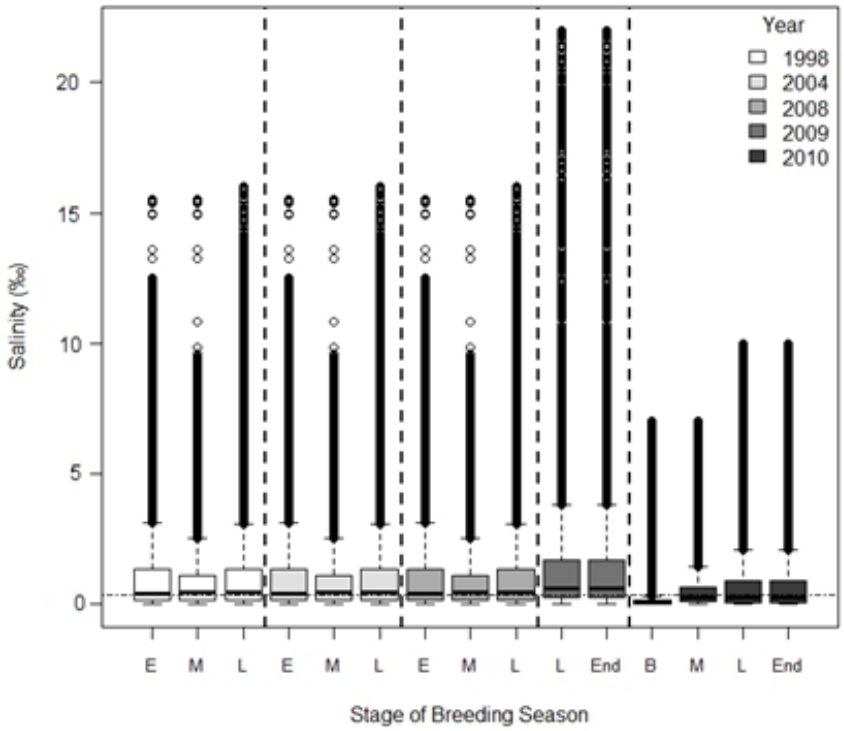


Figure A2.4: Global distribution of SAL values (‰) across the study site for all seasons. 'B': Beginning; 'E': Early; 'M': Mid; 'L': Late. The horizontal dashed line indicates the SAL median for all stages analysed; whiskers show the value farthest from the median that is within 1.5IQR (inter-quartile range) of the upper and lower quartiles respectively.

Table A2.2: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in SAL; *n* for each stage = 82223.

Comparison	t-value	*p*
1998earlv-1998mid	-17.42	< 0.001
1998early-1998late	-0.69	0.767
1998mid-1998late	17.03	< 0.001
2004 early -2004 mid	-17.42	< 0.001
2004early -2004late	-0.69	0.767
2004mid -2004late	17.03	< 0.001
2008early-2008mid	-17.42	< 0.001
2008early-2008late	-0.69	0.767
2008mid-2008late	17.03	< 0.001
2009late-2009end	63.56	< 0.001
2010beginning-2010mid	112.36	< 0.001
2010beginning-2010late	127.97	< 0.001
2010beginning-2010end	127.97	< 0.001
2010mid-2010late	28.27	< 0.001
2010mid-2010end	28.27	< 0.001
2010late-2010end	< 0.01	< 0.001

A2.2 Weather data

The following two tables display the full set of qualitative and quantitative weather data utilised in this research.

Table A2.3: Daily mean MSLP (hPa) and air temperature (°C) recorded on Sule Skerry for each day throughout the five focal breeding seasons. Day 1 = 28th September in all years.

	Year									
	1998		2004		2008		2009		2010	
Day	MSLP (hPa)	Air Temp (°C)	MSLP (hPa)	Air Temp (°C)	MSLP (hPa)	Air Temp (°C)	MSLP (hPa)	Air Temp (°C)	MSLP (hPa)	Air Temp (°C)
1	-	-	-	-	1023.1	11.2	1016.5	11.2	1015.8	11.9
2	1005.4	13.4	1016.7	9.4	1012.6	11.5	1018.2	9.8	1012.3	12.6
3	1007.9	13.3	1012.6	11.3	996.3	10.7	1018.3	9.9	1009.6	11.7
4	1015.0	13.4	1012.8	11.6	989.6	10.1	1015.0	9.6	1003.0	12.0
5	1020.4	13.0	999.0	11.7	995.1	9.1	1015.8	7.6	991.9	11.9
6	1019.5	12.8	997.3	10.8	1007.3	8.0	988.3	10.2	992.9	12.3
7	1018.4	12.3	993.1	10.5	1002.7	7.7	993.2	9.0	988.5	12.3
8	1023.2	11.8	985.7	10.3	991.3	8.5	1007.4	8.1	982.9	12.8
9	1027.8	12.3	983.5	10.2	1004.8	10.0	998.5	10.2	988.4	12.0
10	1029.7	12.2	1002.9	10.8	999.9	11.7	998.4	9.5	1001.2	12.3
11	1030.4	12.4	1020.8	9.5	999.6	12.0	1006.0	8.7	1017.6	12.5
12	1013.6	13.8	1026.8	8.9	1016.1	11.9	1020.1	8.5	1023.0	12.5
13	1002.0	11.3	1025.8	8.9	1009.4	13.1	1009.9	11.0	1024.9	11.8
14	999.1	10.8	1024.1	10.0	1007.4	12.2	1006.0	10.1	1025.6	10.8
15	998.0	10.9	1020.5	10.7	1014.3	11.6	1021.9	10.5	1024.7	10.0
16	1006.9	11.9	1007.9	10.8	1005.4	11.7	1026.3	10.3	1023.5	9.8
17	998.9	11.1	998.2	11.4	1009.2	10.9	1023.8	12.5	1022.8	11.5
18	999.8	9.8	997.4	11.2	1006.8	10.6	1030.5	12.5	1019.1	11.3
19	1012.6	9.2	1007.2	10.7	998.6	9.7	1036.6	10.6	1021.4	10.4
20	1001.2	8.4	1006.9	9.7	1010.0	9.9	1035.5	10.2	1019.9	11.2
21	1007.4	7.7	1002.8	9.3	1003.1	10.7	1020.3	10.8	1006.8	11.1
22	1004.3	8.3	997.8	9.0	1002.0	9.9	1012.6	9.5	1006.5	8.4
23	1012.1	8.0	996.7	8.2	981.5	11.6	1002.0	10.7	1015.4	5.8
24	993.6	10.4	988.1	9.2	985.0	8.6	998.5	11.7	1011.6	6.3
25	-	-	979.1	10.1	998.7	7.1	998.4	11.4	1008.9	7.5
26	989.4	11.4	993.9	10.0	998.2	11.3	1002.5	11.3	1006.3	7.6
27	997.7	10.0	999.9	9.1	988.5	10.1	1005.3	11.9	1013.4	7.2
28	984.2	9.6	994.2	8.9	999.6	9.6	991.3	11.6	1021.1	8.1
29	990.7	7.8	1002.5	8.1	993.7	9.2	1007.1	10.4	1013.3	9.2
30	997.0	8.5	1004.8	8.9	996.2	7.6	1018.4	10.3	994.8	11.2
31	-	-	999.9	10.4	1007.5	4.5	1007.9	11.6	996.8	9.8
32	-	-	996.8	10.7	1002.7	6.4	1013.7	12.6	989.0	11.1
33	-	-	1005.6	11.0	1003.8	7.5	1015.1	12.7	974.5	10.5
34	-	-	1013.9	10.3	1015.4	7.7	1009.0	12.8	988.6	9.7
35	-	-	1020.0	10.5	1017.3	7.3	1004.9	11.8	1009.0	8.7
36	-	-	1022.4	10.6	-	-	982.9	10.2	989.5	9.8
37	-	-	1014.9	10.1	-	-	-	-	984.6	9.6
38	-	-	1002.6	9.8	-	-	-	-	-	-

Table A2.4: Rainfall data for North Rona. Data for 2008 and 2009 represent quantitative measurements (mm), whilst data for 1998, 2004 and 2010 are qualitative observations made by SDT. **D:** Dry; **N:** None; **L:** Light; **M:** Moderate; **H:** Heavy; **O:** Occasional; **F:** Frequent; **C:** Constant. Day 1 = 28th September.

Day	Year				
	1998	2004	2008	2009	2010
1	-	-	-	-	D/N
2	D/N	D/N	-	-	C
3	L/O	L/C	2.7	1.75	D/N
4	D/N	D/N	3.8	1.85	D/N
5	D/N	D/N	6	18	O
6	-	M/O	0	22	-
7	-	L/O	14.5	5	D/N
8	-	D/N	0.7	11	-
9	D/N	M/F	0	16.5	N
10	D/N	L/O	5.5	8	N
11	D/N	D/N	0.9	5	N
12	M/O	D/N	0	4.5	N
13	M/O	D/N	2.1	11	-
14	H/F	D/N	5.5	8	N
15	D/N	D/N	4.5	0	N
16	M/C	D/N	8.4	22	N
17	-	L/O	0	8	N
18	L/O	D/N	2.7	1.8	N
19	-	D/N	0.7	0	-
20	M/O	L/O	0.8	0	N
21	-	M/O	9.2	7	O
22	M/O	D/N	8.8	0.25	H/F
23	D/N	D/N	3.2	0	-
24	M/F	M/C	3.1	2.5	O
25	-	H/O	5.3	2	O
26	H/F	L/O	19.9	2	-
27	H/F	L/O	11.7	2	O
28	M/C	L/O	15.8	2.5	N
29	M/O	L/O	0	0	N
30	-	M/C	0	7	-
31	-	D/N	-	-	M/F
32	-	D/N	2	0	N
33	-	L/O	5.5	3	M/F
34	-	L/O	2.5	-	F
35	-	D/N	-	-	-
36	-	D/N	-	-	N
37	-	D/N	-	-	-

A2.3 Population trends in distribution patterns

A2.3.1 Change in NNdis on focal dates during each breeding season

Overall, mean NNdis increased consistently and significantly over each season (Figure 3.10; MULTCOMP: **1998:** $F_{2,1079}$= 47.39, $p < 0.001$; **2004:** $F_{2,608}$=21.92, $p < 0.001$; **2008:** $F_{2,553}$= 30.62, $p < 0.001$; **2009:** $F_{1,284}$= 13.43, $p < 0.001$; **2010:** $F_{3,200}$= 6.63, $p < 0.001$). Post-hoc MULTCOMP comparisons (Table A2.5) indicated significant differences between stages within each season.

Table A2.5: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in NNdis.

Comparison	t-value	*p*
1998early-1998mid	7.06	< 0.001
1998early-1998late	8.11	< 0.001
1998mid-1998late	1.47	< 0.001
2004 early -2004 mid	4.35	< 0.001
2004early -2004late	6.42	< 0.001
2004mid -2004late	2.76	< 0.001
2008early-2008mid	3.42	< 0.001
2008early-2008late	7.46	< 0.001
2008mid-2008late	4.87	< 0.001
2009late-2009end	3.83	< 0.001
2010beginning-2010mid	1.40	< 0.001
2010beginning-2010late	1.87	< 0.001
2010beginning-2010end	4.35	< 0.001
2010mid-2010late	0.73	< 0.001
2010mid-2010end	4.08	< 0.001
2010late-2010end	3.26	< 0.001

A2.3.2 Change in MPdis on focal dates during each breeding season

MULTCOMP analysis showed that there were no significant differences in mother-pup distances between stages within each breeding season (Figures 3.11), with the exception of 2004 (**1998:** $F_{2,399}$= 0.76, p = 0.468; **2004:** $F_{2,293}$=4.911, p = 0.008; **2008:** $F_{2,218}$= 1.68, p = 0.189; **2009:** $F_{1,115}$= 0.00, p = 0.990; **2010:** $F_{3,339}$= 1.04, p = 0.377). Post-hoc multiple comparisons revealed a significant decrease in mother-pup distance between early-mid and early-late 2004 (**2004 early - 2004 mid:** t=-2.82, p = 0.014, **2004 early -2004late:** t= -3.00, p = 0.008, **2004 mid -2004late:** t= -0.31, p = 0.948).

A2.3.3 Change in MPdis throughout each breeding season

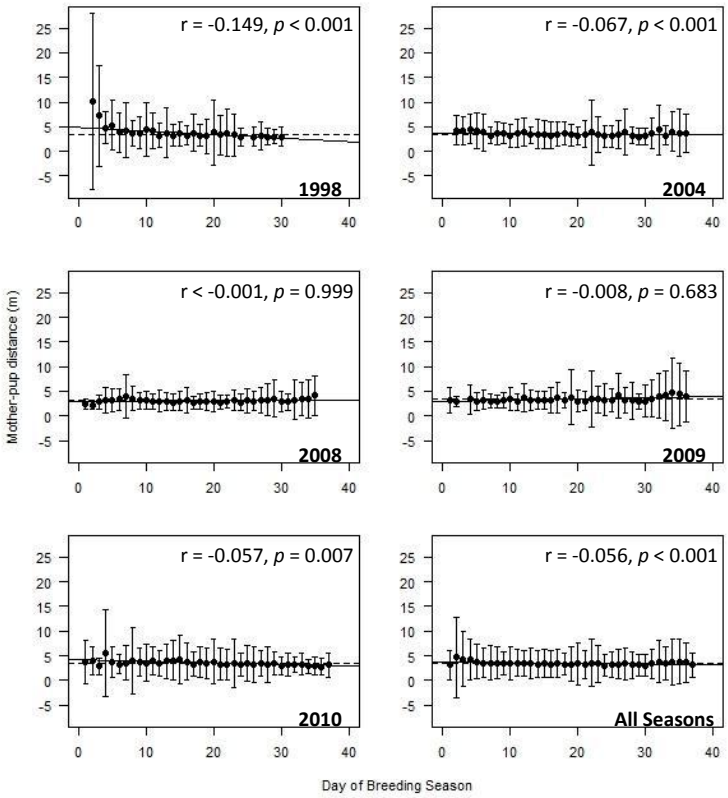


Figure A2.5 Change in mother-pup distance (m) over every day in all five breeding seasons. In all years, Day 1 = 28th September. Pearson's product-moment correlation indicates a significant but negligible and inconsistent correlation in 1998, 2004 and 2010, taking into account only the daily means. Solid line represents regression line of best fit whilst the dashed line indicates the seasonal mean MPdis.

A2.3.3 Nearest-neighbour analysis

This section details the analyses performed on NNdis data for all days of each breeding season. Table A2.3 provides a summary of daily mean nearest neighbour distances extracted from the GIS database. The observed mean NNdis ($\bar{d}_{obs}$) is lower than would be expected if the seals were distributed randomly or in a maximally dispersed arrangement over the study site on every date.

Table A2.6: Summary of daily mean nearest neighbour distances ($\bar{d}_{obs}$ compared to $\bar{d}_{ran}$ and $\bar{d}_{dis}$ for each day throughout the five breeding seasons). Day 1 = 28th September.

Day	Observed and theoretical NNdis (m) by year														
	1998			2004			2008			2009			2010		
	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$
1	-	-	-	-	-	-	4.13	21.61	46.45	4.46	17.39	37.36	7.07	24.96	53.64
2	5.72	18.21	39.13	6.29	16.03	34.45	4.05	18.36	39.45	6.26	17.78	38.22	8.55	21.37	45.93
3	7.53	17.78	38.22	6.79	15.64	33.62	3.37	15.03	32.30	6.58	18.21	39.13	5.41	20.91	44.94
4	8.18	16.90	36.31	5.41	14.34	30.81	4.49	15.55	33.42	4.83	13.80	29.65	7.88	18.67	40.11
5	6.94	14.79	31.78	5.32	12.67	27.23	5.70	13.37	28.73	3.99	13.86	29.79	7.34	17.39	37.36
6	6.09	13.55	29.11	4.24	12.07	25.95	4.54	11.20	24.06	5.64	12.43	26.72	6.62	15.83	34.03
7	5.38	12.77	27.45	5.86	10.84	23.29	5.00	12.16	26.13	4.02	10.51	22.59	5.48	14.87	31.95
8	5.85	11.95	25.68	5.72	10.57	22.71	4.41	10.72	23.03	4.93	10.78	23.16	6.11	14.27	30.66
9	5.18	12.07	25.95	5.35	10.01	21.52	4.67	11.16	23.99	5.50	11.55	24.83	6.24	13.20	28.36
10	5.22	12.12	26.04	5.02	9.80	21.06	5.19	11.95	25.68	5.14	10.84	23.29	5.57	12.77	27.45
11	4.59	11.09	23.84	4.78	9.41	20.23	5.03	11.95	25.68	5.57	10.84	23.29	5.22	13.03	28.01
12	4.50	9.50	20.41	4.88	9.67	20.77	5.82	11.20	24.06	5.09	10.63	22.84	5.90	12.57	27.02
13	4.15	8.35	17.94	5.25	10.06	21.63	5.41	10.75	23.09	4.94	10.32	22.18	4.67	12.03	25.86
14	4.85	8.35	17.94	5.13	9.97	21.42	5.39	10.54	22.65	5.55	10.09	21.68	5.98	12.16	26.13
15	4.28	7.48	16.08	4.85	9.64	20.73	6.03	10.04	21.57	5.51	10.29	22.12	5.68	12.39	26.62
16	5.05	7.93	17.04	4.67	9.54	20.50	5.64	10.14	21.79	6.73	10.57	22.71	6.48	12.62	27.13
17	4.82	7.73	16.61	5.23	8.98	19.30	4.47	9.52	20.45	5.95	10.27	22.06	5.04	11.83	25.41
18	5.34	7.86	16.88	5.37	9.03	19.41	5.67	10.24	22.01	6.17	10.16	21.84	5.36	11.48	24.67
19	4.86	7.37	15.85	5.05	8.94	19.22	5.06	10.01	21.52	5.03	10.14	21.79	5.36	11.44	24.59
20	4.81	7.40	15.91	5.48	8.96	19.26	5.24	10.06	21.63	5.64	10.24	22.01	6.30	11.79	25.33
21	4.83	7.33	15.74	5.13	8.71	18.72	5.45	9.87	21.21	5.79	9.99	21.47	6.36	11.20	24.06
22	5.12	7.20	15.48	5.06	8.74	18.79	5.97	9.67	20.77	5.13	10.01	21.52	5.28	10.63	22.84
23	4.75	6.92	14.88	5.38	9.07	19.49	5.60	9.64	20.73	5.71	9.78	21.01	5.78	10.78	23.16
24	5.46	7.02	15.09	5.06	10.29	22.12	5.93	9.58	20.59	6.32	9.99	21.47	6.67	10.90	23.43
25	-	-	-	5.43	9.01	19.37	5.45	9.56	20.54	6.24	9.97	21.42	5.32	10.66	22.90
26	5.21	7.61	16.35	5.89	9.01	19.37	6.40	10.11	21.73	5.92	10.48	22.53	6.33	11.13	23.91
27	5.43	7.17	15.41	5.27	9.16	19.68	7.44	10.24	22.01	6.54	10.87	23.36	6.34	10.84	23.29
28	5.26	7.02	15.09	6.35	9.56	20.54	6.94	11.67	25.07	6.99	11.09	23.84	5.98	11.55	24.83
29	5.12	7.18	15.43	5.98	9.87	21.21	7.07	10.21	21.95	6.83	10.43	22.41	7.54	11.52	24.75
30	5.91	7.58	16.28	6.42	10.06	21.63	7.49	10.54	22.65	7.02	11.30	24.28	7.55	11.71	25.16
31	-	-	-	6.90	10.54	22.65	8.36	11.41	24.51	7.69	11.91	25.59	7.27	12.12	26.04
32	-	-	-	6.49	10.72	23.03	7.70	10.87	23.36	8.17	12.16	26.13	8.51	12.57	27.02
33	-	-	-	6.22	10.78	23.16	7.88	11.79	25.33	8.47	12.72	27.34	8.21	12.48	26.82
34	-	-	-	7.98	11.99	25.77	8.84	12.39	26.62	8.89	12.82	27.56	9.46	13.03	28.01
35	-	-	-	6.24	10.84	23.29	8.99	13.03	28.01	8.73	13.09	28.13	8.48	12.67	27.23
36	-	-	-	7.02	11.79	25.33	-	-	-	8.68	13.61	29.25	9.38	13.37	28.73
37	-	-	-	7.84	12.16	26.13	-	-	-	-	-	-	9.40	13.99	30.07
38	-	-	-	8.23	12.16	26.13	-	-	-	-	-	-	-	-	-

Table A2.3 summarises the values for the nearest neighbour index, *R*, calculated for each day of all breeding seasons. The change in *R* indicates that females are initially clustered early in each breeding season but become more dispersed as the season progresses. Tables A1.1 and A1.2 provide critical values for two methods of assessing the significance of *R* (Section 3.2.3).

Table A2.7: Daily nearest-neighbour index, *R*, values calculated for all breeding seasons. See Figure 3.17 in Chapter 3.3. In each year, Day 1 = 28th September.

Day of breeding season	Year					Day of breeding season	Year				
	1998	2004	2008	2009	2010		1998	2004	2008	2009	2010
1	-	-	0.191	0.256	0.283	**20**	0.750	0.575	0.726	0.602	0.585
2	0.431	0.513	0.435	0.474	0.436	**21**	0.713	0.664	0.594	0.630	0.518
3	0.413	0.508	0.421	0.514	0.401	**22**	0.423	0.606	0.692	0.655	0.655
4	0.474	0.505	0.520	0.479	0.470	**23**	0.780	0.434	0.224	0.361	0.258
5	0.498	0.522	0.504	0.478	0.388	**24**	0.484	0.638	0.711	0.622	0.645
6	0.581	0.515	0.511	0.551	0.492	**25**	-	0.654	0.733	0.646	0.600
7	0.571	0.503	0.601	0.535	0.459	**26**	0.469	0.606	0.708	0.672	0.677
8	0.637	0.489	0.556	0.637	0.513	**27**	0.449	0.577	0.669	0.666	0.658
9	0.624	0.582	0.470	0.580	0.426	**28**	0.421	0.665	0.714	0.694	0.726
10	0.679	0.595	0.554	0.607	0.467	**29**	0.489	0.576	0.690	0.667	0.669
11	0.659	0.565	0.505	0.496	0.468	**30**	0.429	0.595	0.289	0.638	0.702
12	0.314	0.392	0.221	0.352	0.400	**31**	-	0.644	0.426	0.350	0.672
13	0.650	0.611	0.521	0.551	0.534	**32**	-	0.677	0.405	0.288	0.422
14	0.659	0.589	0.553	0.579	0.568	**33**	-	0.377	0.411	0.454	0.422
15	0.711	0.579	0.617	0.512	0.497	**34**	-	0.420	0.411	0.382	0.418
16	0.686	0.593	0.581	0.584	0.536	**35**	-	0.351	0.419	0.458	0.369
17	0.778	0.492	0.619	0.632	0.611	**36**	-	0.540	-	-	0.428
18	0.685	0.602	0.570	0.626	0.499	**37**	-	0.541	-	-	0.473
19	0.758	0.653	0.633	0.564	0.569	**38**	-	0.534	-	-	-

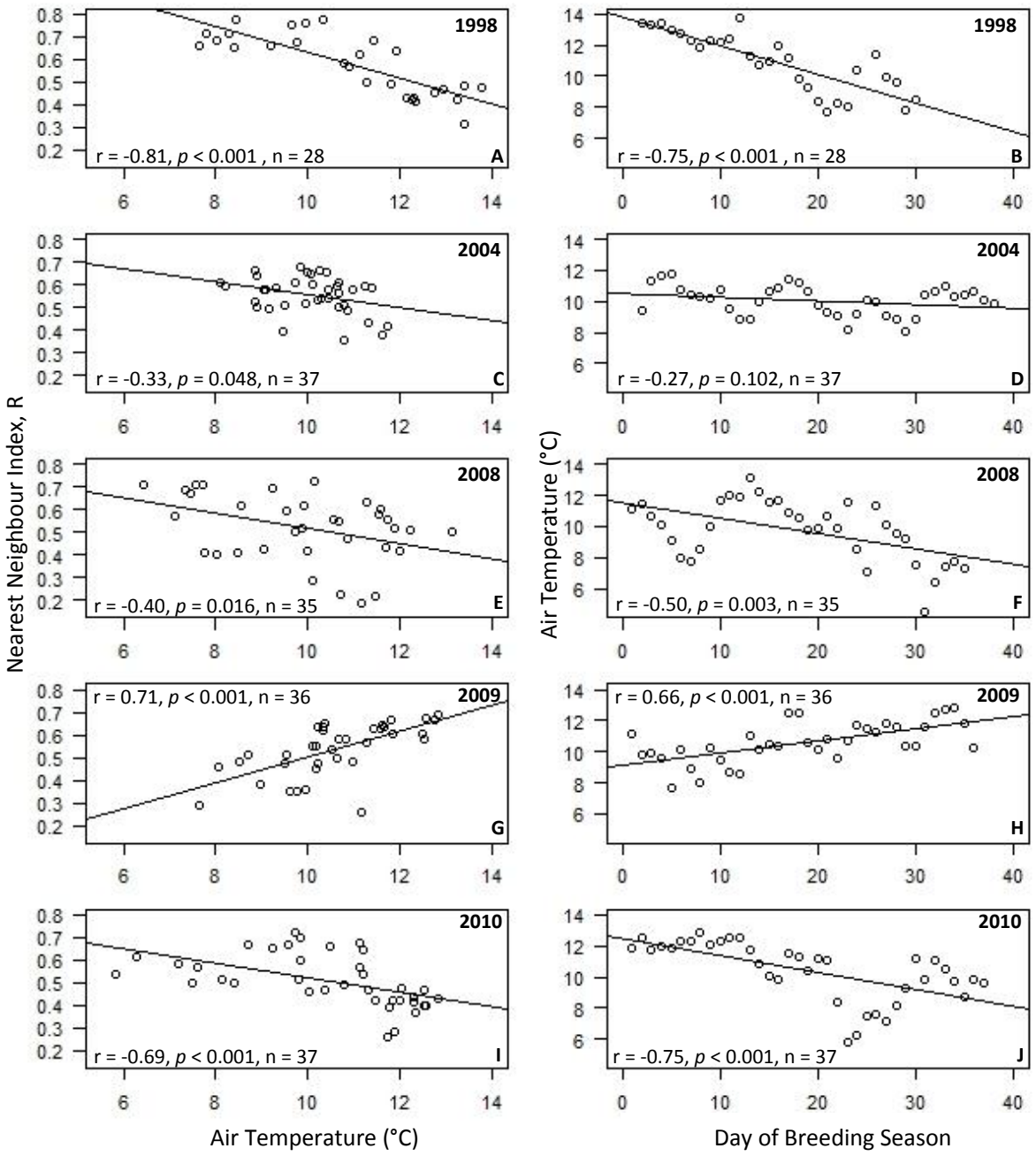


Figure A2.6: Relationship between air temperature (°C) and nearest neighbour index, R (**A, C, E, G, I**) and between air temperature (°C) and day of breeding season (**B, D, F, H, J**). Comparison of Spearman's rank correlation coefficients demonstrates that R only correlates with air temperature during years in which air temperature also correlates strongly with day of breeding season. Solid line represents linear regression line of best fit.

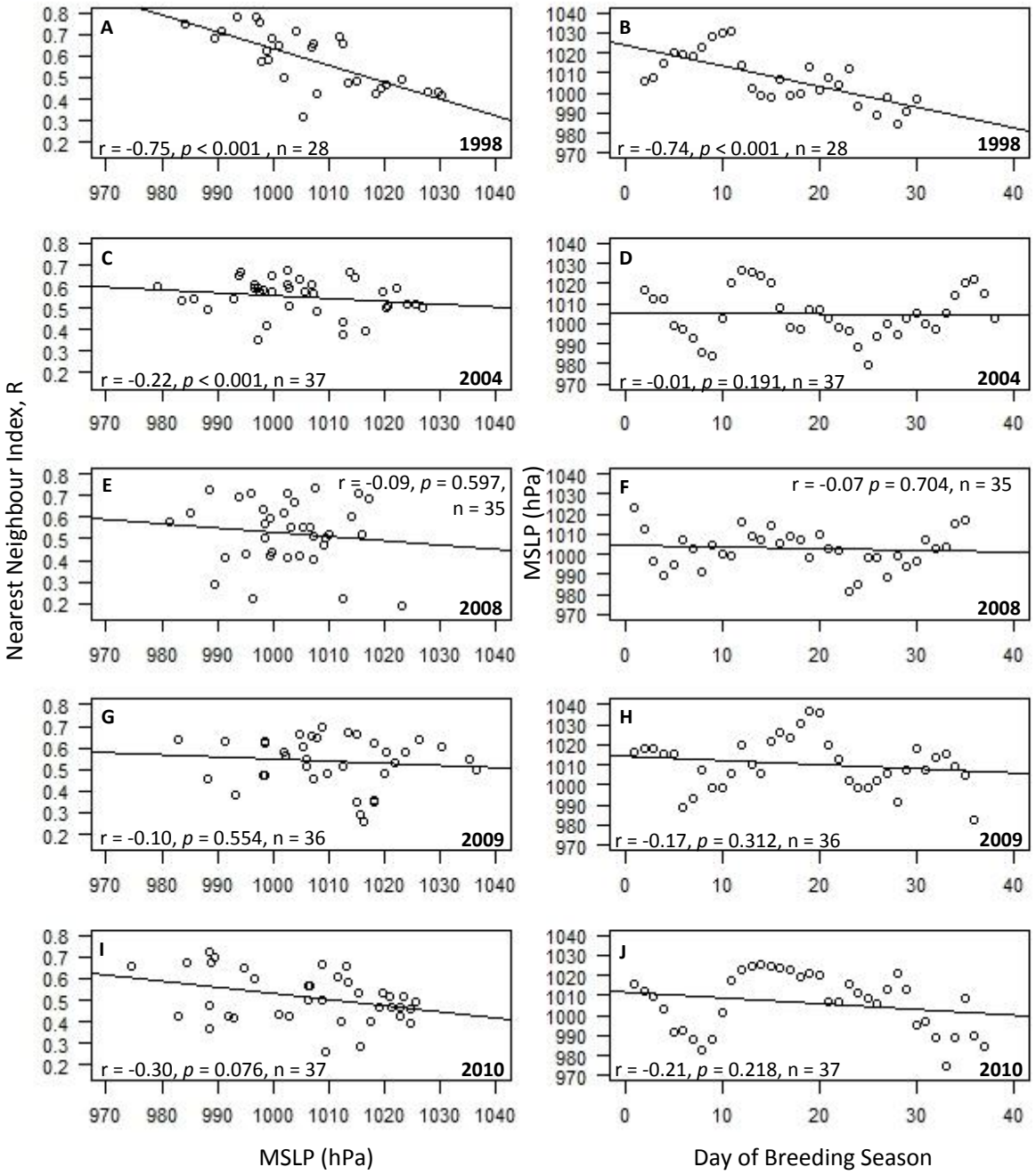


Figure A2.7: Relationship between MSLP (hPa) and nearest neighbour index, R (**A, C, E, G, I**) and between MSLP (hPa) and day of breeding season (**B, D, F, H, J**). Comparison of Spearman's rank correlation coefficients demonstrates that R only correlates with MSLP during years in which MSLP also correlates strongly with day of breeding season. Solid line represents linear regression line of best fit.

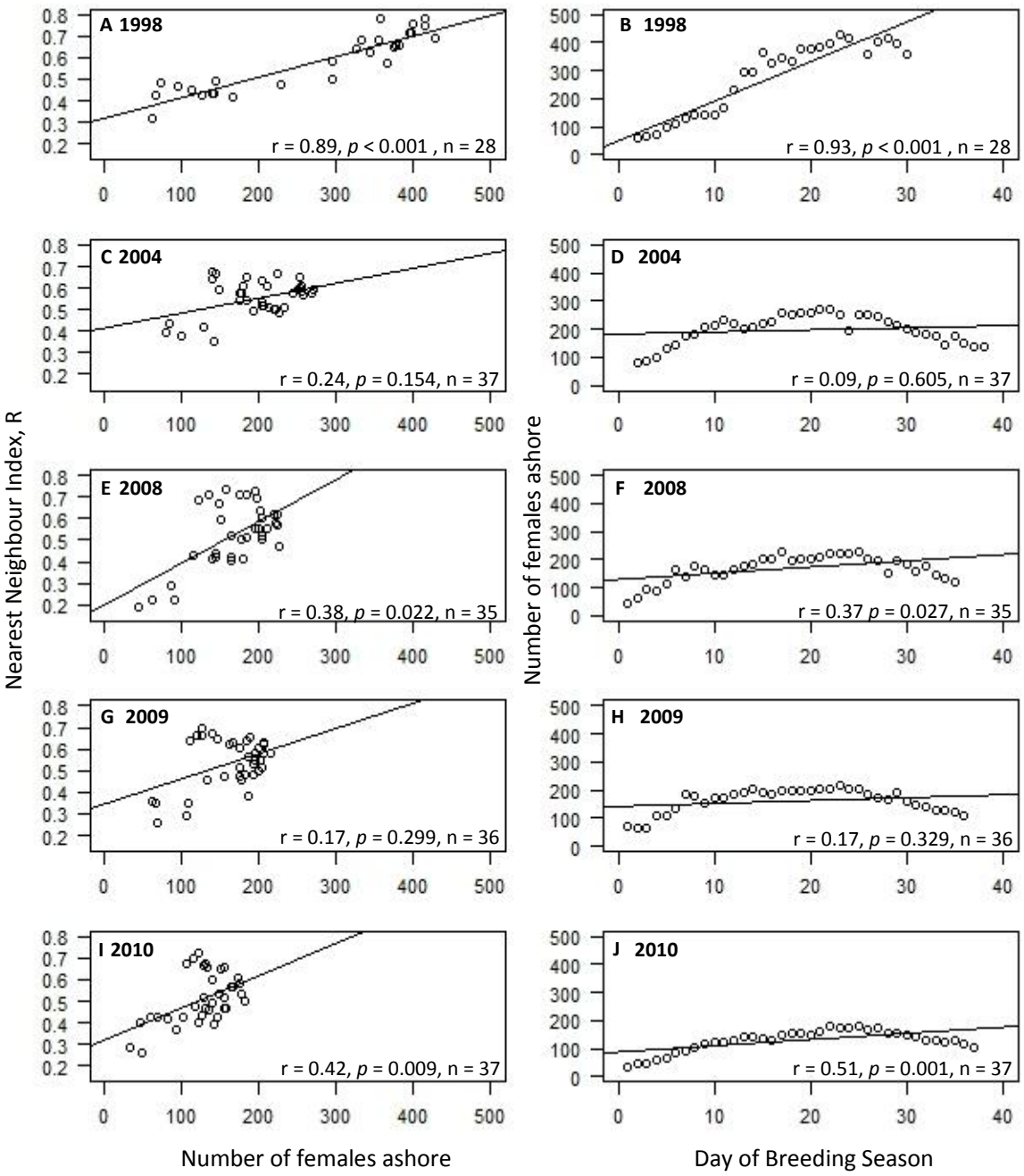


Figure A2.8: Relationship between count of females ashore and nearest neighbour index, R (**A, C, E, G, I**) and between count ashore and day of breeding season (**B, D, F, H, J**). Comparison of Spearman's rank correlation coefficients demonstrates that R only correlates with count ashore during years in which count ashore also correlates strongly with day of breeding season. Solid line represents linear regression line of best fit.

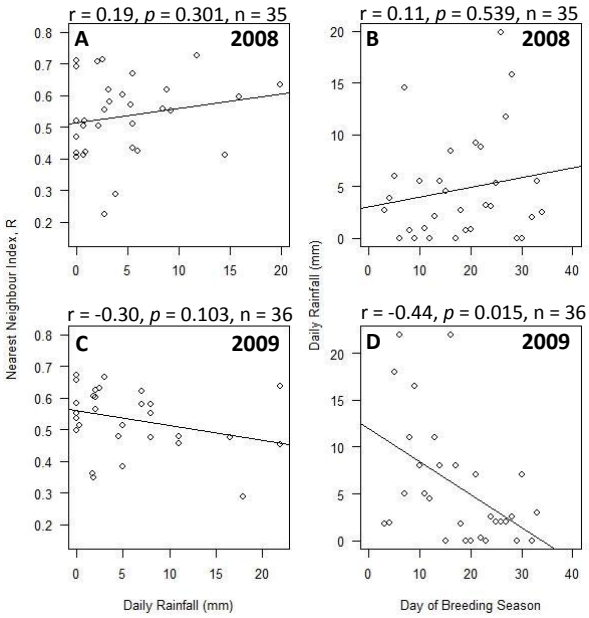


Figure A2.9: Relationship between daily rainfall (mm) and nearest neighbour index, R (**A, C**) and between daily rainfall (mm) and day of breeding season (**B, D**). Solid line represents linear regression line of best fit. Spearman's rank correlation shows that rainfall is only correlated with day of breeding season in 2009, but not with day of breeding season in 2008 or nearest neighbour index in either year.

A2.4 Habitat associations of grey seals

A2.4.1 Elevation

There is substantial variation around the female and pup means, with significant differences in female ELEV values between stages within the 1998, 2004 and 2008 breeding seasons (Figure A2.10; MULTCOMP; **1998:** $F_{2,1079}$= 18.90, p < 0.001; **2004:** $F_{2,608}$=4.98, p = 0.007; **2008:** $F_{2,553}$= 15.37, p < 0.001; **2009:** $F_{2,284}$= 0.57, p = 0.452; **2010:** $F_{3,459}$= 2.125, p = 0.096). Post-hoc multiple comparisons of the female location data demonstrate that, where there are significant changes in ELEV within a breeding season, the average ELEV of female locations increases as the season progresses (Table A2.8). The same was true of pup locations (Figure A2.10; MULTCOMP; **1998:** $F_{2,432}$= 2.846, p = 0.059; **2004:** $F_{2,329}$=3.61, p = 0.028; **2008:** $F_{2,240}$= 4.07, p = 0.018; **2009:** $F_{2,128}$= 0.028, p = 0.867; **2010:** $F_{3,200}$= 1.08, p = 0.36). Post-hoc multiple comparisons of the pup location data demonstrate that, where there are significant changes in ELEV used over a breeding season, the average ELEV of pup locations increases as the season progresses (Table A2.9). The 2004 breeding season was the only exception to these trends for both females and pups; in 2004, females and pups were found at higher elevation in the middle of the breeding season.

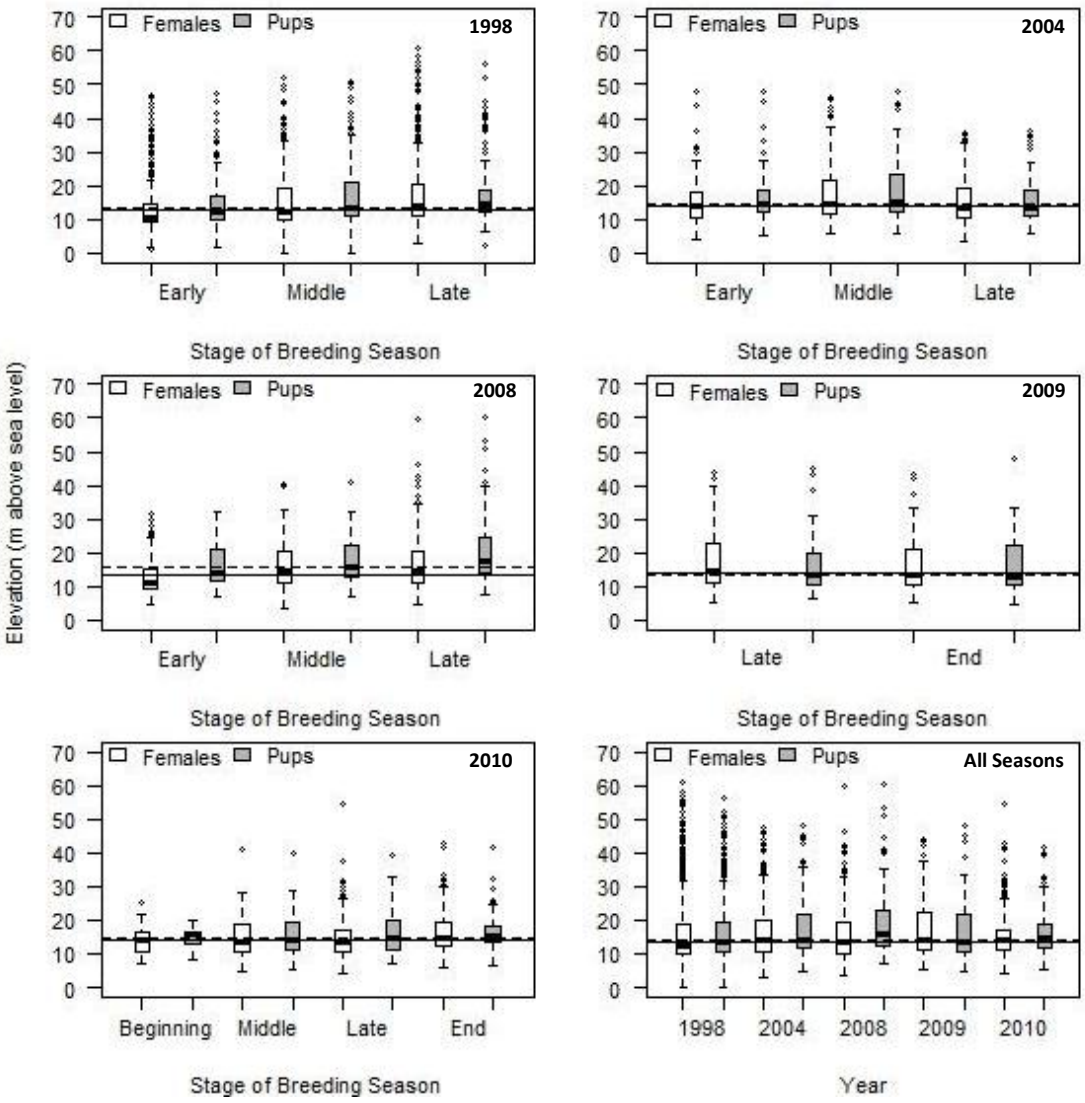


Figure A2.10: Female and pup distribution on elevation values (in metres above sea level) during each breeding season stage. On all graphs the horizontal dashed line represents the pup median over the season and the solid horizontal line represents the female median.

Table A2.8: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in ELEV values at female locations.

Comparison	t-value	*p*
1998early-1998mid	-2.77	0.015
1998early-1998late	-6.13	< 0.001
1998mid-1998late	-3.49	0.002
2004 early -2004 mid	-2.78	0.015
2004early -2004late	-0.57	0.837
2004mid -2004late	2.48	0.036
2008early-2008mid	-5.15	< 0.001
2008early-2008late	-4.78	< 0.001
2008mid-2008late	-0.35	0.935
2009late-2009end	0.747	0.456
2010beginning-2010mid	-1.17	0.641
2010beginning-2010late	-0.97	0.766
2010beginning-2010end	-2.58	0.049
2010mid-2010late	0.26	0.994
2010mid-2010end	-1.67	0.340
2010late-2010end	-1.92	0.219

Table A2.9: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in ELEV values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	-1.46	0.309
1998early-1998late	-2.43	0.040
1998mid-1998late	-1.18	0.465
2004 early -2004 mid	-0.95	0.604
2004early -2004late	1.17	0.471
2004mid -2004late	2.73	0.018
2008early-2008mid	-1.13	0.495
2008early-2008late	-2.56	0.029
2008mid-2008late	-1.92	0.132
2009late-2009end	0.17	0.869
2010beginning-2010mid	-0.37	0.984
2010beginning-2010late	-1.19	0.629
2010beginning-2010end	-1.62	0.365
2010mid-2010late	-1.00	0.750
2010mid-2010end	-1.48	0.449
2010late-2010end	-0.57	0.939

Figures A2.11 and A2.12 suggest that the ELEV at sites occupied by females does not influence their NNdis (Pearson's product moment correlation; r = 0.179, df = 2996, $p < 0.001$) or MPdis (Pearson's product moment correlation; r = 0.060, df = 1218, $p = 0.035$).

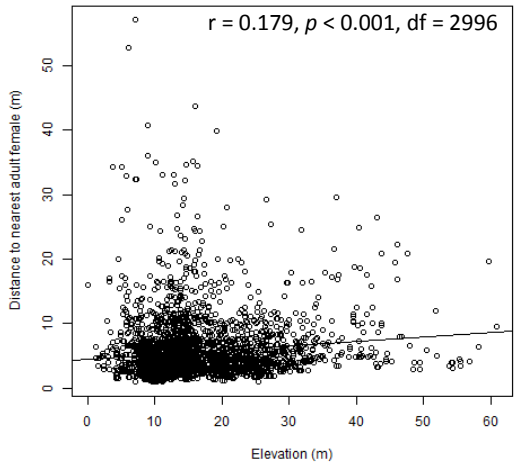


Figure A2.11: Correlation of elevation values with nearest neighbour distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows little relationship between the elevation of sites occupied by females and their NNdis.

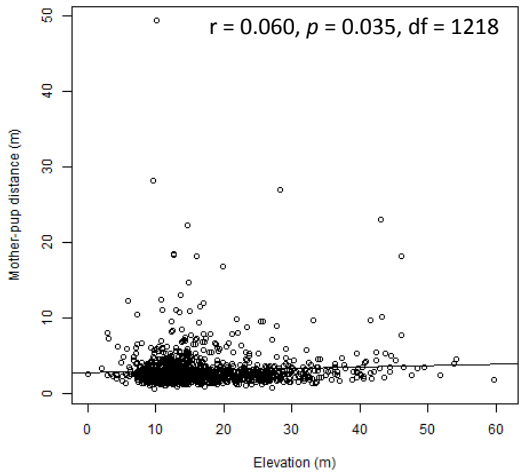


Figure A2.12: Correlation of elevation values with mother-pup distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows little relationship between the elevation of sites occupied by females and the distance to 'their' pup.

A2.4.2 Cost-distance to access

There is considerable variation around the female and pup means, with significant differences in female CACC values between stages within all breeding seasons except 2009 (Figure A2.13; MULTCOMP; **1998:** $F_{2,1079}$= 18.69, $p < 0.001$; **2004:** $F_{2,608}$=5.64, $p = 0.004$; **2008:** $F_{2,553}$= 17.63, $p < 0.001$; **2009:** $F_{2,284}$= 0.18, $p = 0.676$; **2010:** $F_{3,459}$= 4.28, $p = 0.005$). Post-hoc multiple comparisons of the female location data demonstrate that, where there are significant changes in CACC of used locations within a breeding season, the average CACC of female locations increases as the season progresses; in other words, females move further inland (further from access points) as the season progresses (Table A2.10). The same was true for pups, which showed significant differences in within-season CACC values in 1998, 2004 and 2008 (Figure A2.13; MULTCOMP; **1998:** $F_{2,432}$= 3.77, $p = 0.024$; **2004:** $F_{2,329}$=3.18, $p = 0.043$; **2008:** $F_{2,240}$= 4.89, $p = 0.008$; **2009:** $F_{2,128}$= 0.039, $p = 0.843$; **2010:** $F_{3,200}$= 2.35, $p = 0.074$). Post-hoc multiple comparisons of the pup location data demonstrate that, where there are significant changes in CACC of pup locations over a breeding season, the average CACC of pup locations generally increases as the season progresses (Table A2.11). The 2004 breeding season was the only exception to these trends for both females and pups; in 2004, females and pups were found at further inland in the middle of the breeding season.

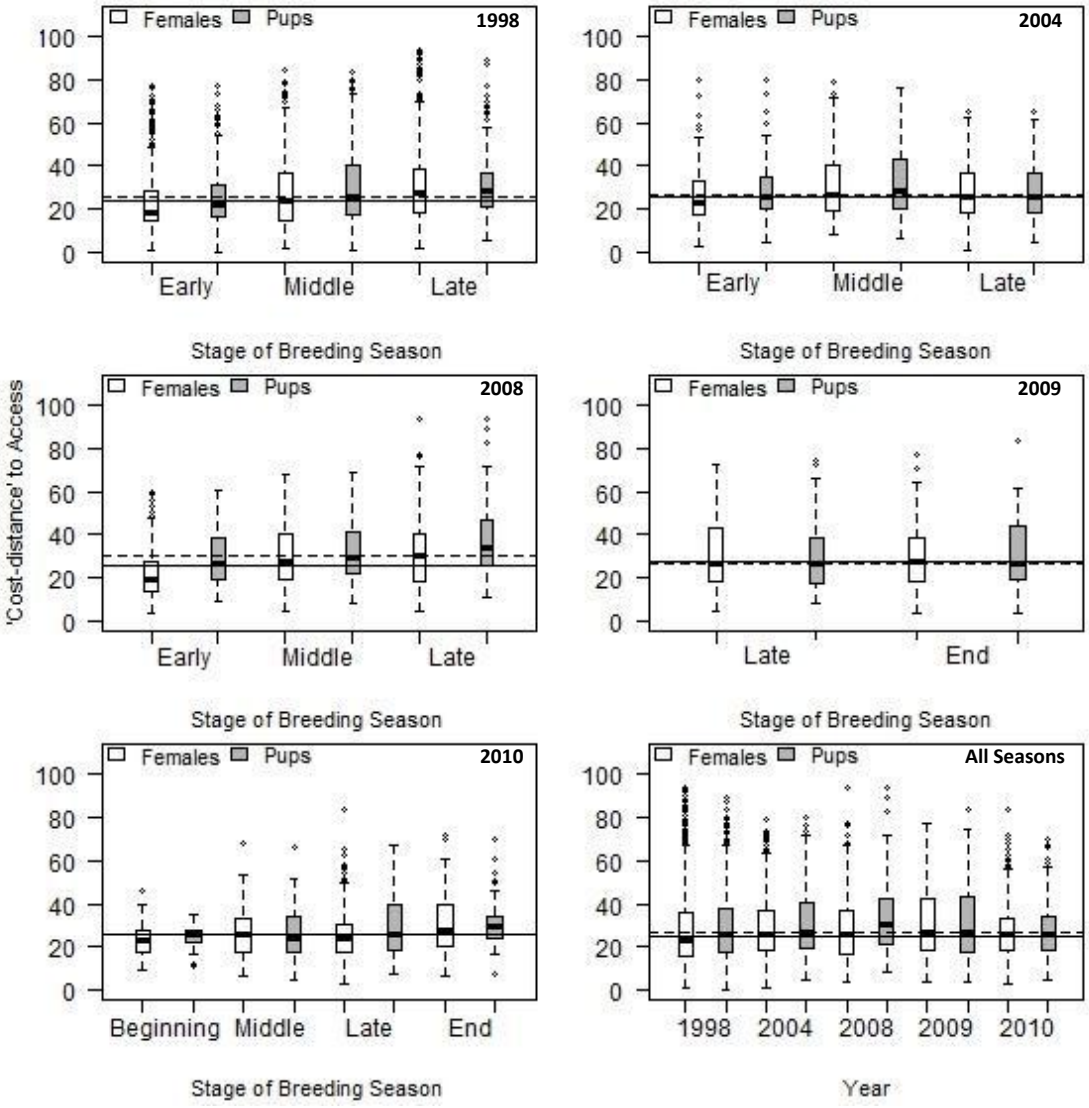


Figure A2.13: Female and pup distribution on cost-distance to access values during each breeding season stage. On all graphs the horizontal dashed line represents the pup median over the season and the solid horizontal line represents the female median.

Table A2.10: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in CACC values at adult female locations.

Comparison	t-value	*p*
1998early-1998mid	-2.96	0.009
1998early-1998late	-6.09	< 0.001
1998mid-1998late	-3.28	0.003
2004 early -2004 mid	-3.38	0.002
2004early -2004late	-1.68	0.281
2004mid -2004late	1.78	0.176
2008early-2008mid	-5.10	< 0.001
2008early-2008late	-5.29	< 0.001
2008mid-2008late	0.78	0.713
2009late-2009end	0.415	0.679
2010beginning-2010mid	-1.50	0.437
2010beginning-2010late	-1.28	0.578
2010beginning-2010end	-3.65	0.002
2010mid-2010late	0.28	0.993
2010mid-2010end	-2.50	0.060
2010late-2010end	-2.78	0.028

Table A2.11: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in CACC values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	-1.60	0.247
1998early-1998late	-2.77	0.016
1998mid-1998late	-1.45	0.315
2004 early -2004 mid	-1.51	0.287
2004early -2004late	0.43	0.900
2004mid -2004late	2.41	0.043
2008early-2008mid	-1.20	0.449
2008early-2008late	-2.80	0.015
2008mid-2008late	-2.16	0.079
2009late-2009end	-0.19	0.847
2010beginning-2010mid	-0.33	0.988
2010beginning-2010late	-1.50	0.439
2010beginning-2010end	-2.55	0.055
2010mid-2010late	-1.33	0.541
2010mid-2010end	-2.49	0.065
2010late-2010end	-1.08	0.698

Figures A2.14 and A2.15 suggest that the CACC at sites occupied by females does not influence their NNdis (Pearson's product moment correlation; r = 0.189, df = 2996, $p < 0.001$) or MPdis (Pearson's product moment correlation; r = 0.042, df = 1218, $p = 0.147$).

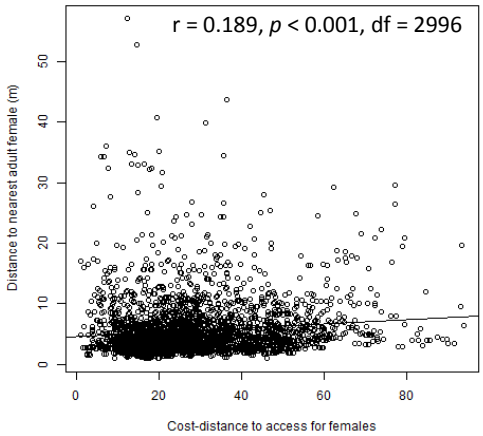


Figure A2.14: Correlation of CACC values with nearest neighbour distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows little relationship between the CACC of sites occupied by females and the distance to their nearest neighbour.

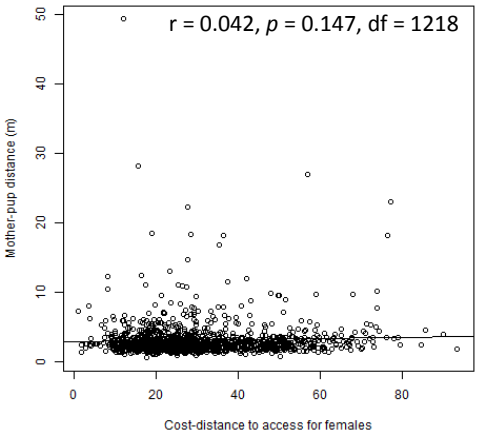


Figure A2.15: Correlation of CACC values with mother-pup distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows no relationship between the CACC of sites occupied by females and the distance to 'their' pup.

A2.4.3 Cost-distance to pool

There are significant differences in female CPOOL values between stages within all breeding seasons (Figure A2.16; MULTCOMP; **1998:** $F_{2,1079}$= 15.05, $p < 0.001$; **2004:** $F_{2,608}$=15.46, $p < 0.001$; **2008:** $F_{2,553}$= 5.61, $p = 0.004$; **2009:** $F_{2,284}$= 23.61, $p < 0.001$; **2010:** $F_{3,459}$= 6.22, $p < 0.001$). Where there are significant changes in CPOOL at used locations within a breeding season, females are typically found further from pools of water as the season progresses (Table A2.12). The same was true for pups, which showed significant differences in within-season CPOOL values in all years except 2008 (Figure A2.16; MULTCOMP; **1998:** $F_{2,432}$= 7.49, $p < 0.001$; **2004:** $F_{2,329}$=5.01, $p = 0.007$; **2008:** $F_{2,240}$= 0.21, $p = 0.810$; **2009:** $F_{2,128}$= 4.41, $p = 0.038$; **2010:** $F_{3,200}$= 3.40, $p = 0.019$). Post-hoc multiple comparisons of the pup location data demonstrate that, where there are significant changes in CPOOL over a breeding season, pups are typically found further from pools later in the season than earlier in the season (Table A2.13). There are a number of exceptions to this trend for both females and pups: in 1998, females and pups were found closer to pools in the middle of the breeding season than early or late in the season, whilst in 2008 females were found closer to pools in the middle of the season than early in the season. Finally, both females and pups were found significantly closer to pools at the end of 2009 than in late 2009. Figures A2.17 and A2.18 suggest that the CPOOL at sites occupied by females does not influence their distance to nearest female neighbour (Pearson's product moment correlation; r = 0.049, df = 2996, $p = 0.007$) or nearest pup (Pearson's product moment correlation; r = 0.028, df = 1218, $p = 0.330$).

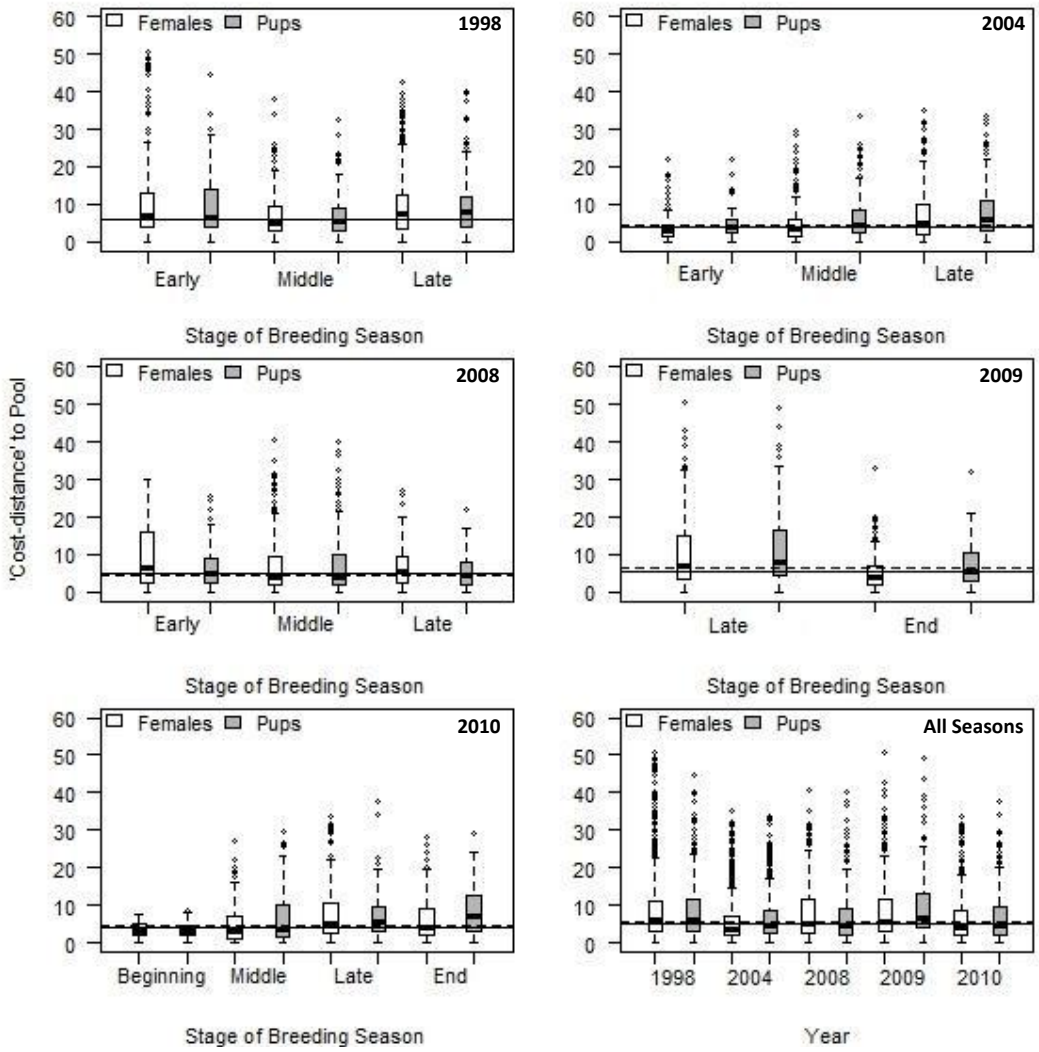


Figure A2.16: Female and pup distribution on cost-distance to pool values during each breeding season stage. On all graphs the horizontal dashed line represents the pup median over the season and the solid horizontal line represents the female median.

Table A2.12: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in CPOOL values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	4.99	< 0.001
1998early-1998late	0.84	0.678
1998mid-1998late	-4.54	< 0.001
2004 early -2004 mid	-1.73	0.196
2004early -2004late	-5.31	< 0.001
2004mid -2004late	-4.05	< 0.001
2008early-2008mid	3.17	0.004
2008early-2008late	2.17	0.077
2008mid-2008late	-1.15	0.487
2009late-2009end	4.99	< 0.001
2010beginning-2010mid	-0.72	0.888
2010beginning-2010late	-4.48	< 0.001
2010beginning-2010end	-2.48	0.065
2010mid-2010late	-3.61	0.002
2010mid-2010end	-1.77	0.289
2010late-2010end	1.46	0.461

Table A2.13: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in CPOOL values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	2.67	0.021
1998early-1998late	0.42	0.906
1998mid-1998late	-3.63	< 0.001
2004 early -2004 mid	-0.82	0.693
2004early -2004late	-3.02	0.008
2004mid -2004late	-2.45	0.031
2008early-2008mid	0.10	0.994
2008early-2008late	0.60	0.822
2008mid-2008late	0.59	0.825
2009late-2009end	2.11	0.037
2010beginning-2010mid	-1.41	0.492
2010beginning-2010late	-2.85	0.025
2010beginning-2010end	-2.95	0.018
2010mid-2010late	-1.85	0.248
2010mid-2010end	-2.06	0.166
2010late-2010end	-0.56	0.942

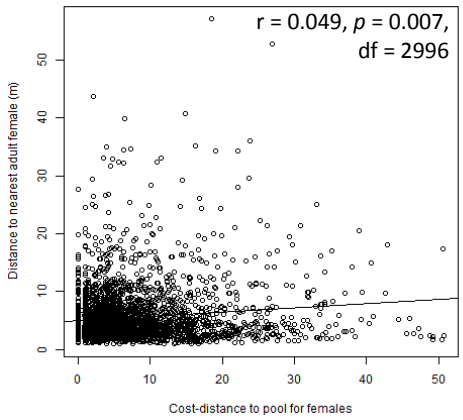


Figure A2.17: Correlation of cost-distance to pool values with nearest neighbour distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows little relationship between the cost-distance to pool of sites occupied by females and the distance to their nearest neighbour.

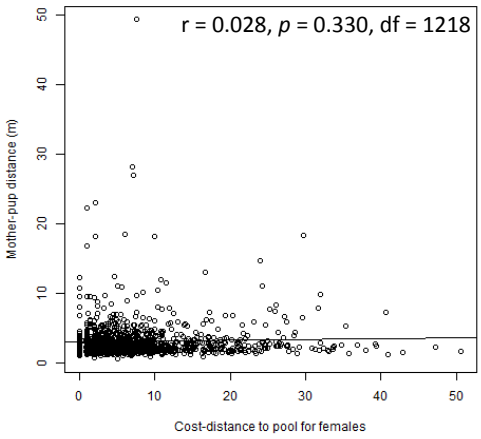


Figure A2.18: Correlation of cost-distance to pool values with mother-pup distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows no relationship between the cost-distance to pool of sites occupied by females and the distance to 'their' pup.

A2.4.4 Salinity

There are significant differences in female SAL values between stages within all breeding seasons except 2009 (Figure A2.19; MULTCOMP; **1998:** $F_{2,1079}$= 21.59, p < 0.001; **2004:** $F_{2,608}$=20.58, p < 0.001; **2008:** $F_{2,553}$= 21.84, p < 0.001; **2009:** $F_{2,284}$= 0.00, p = 0.961; **2010:** $F_{3,459}$= 13.14, p < 0.001). Females were typically found in areas of higher salinity as each season progressed (Table A2.14). The same was true for pups, which showed significant differences in within-season SAL values in 1998 and 2010 (Figure A2.19; MULTCOMP; **1998:** $F_{2,432}$= 13.39, p < 0.001; **2004:** $F_{2,329}$=0.42, p = 0.658; **2008:** $F_{2,240}$= 0.91, p = 0.405; **2009:** $F_{2,128}$= 0.94, p = 0.335; **2010:** $F_{3,200}$= 13.14, p < 0.001). Pups were typically found in areas of higher salinity as each season progressed (Table A2.15). Figures A2.20 and A2.21 suggest that the SAL at sites occupied by females does not influence their distance to nearest female neighbour (Pearson's product moment correlation; r = 0.070, df = 2996, p < 0.001) or nearest pup (Pearson's product moment correlation; r = 0.026, df = 1218, p = 0.370).

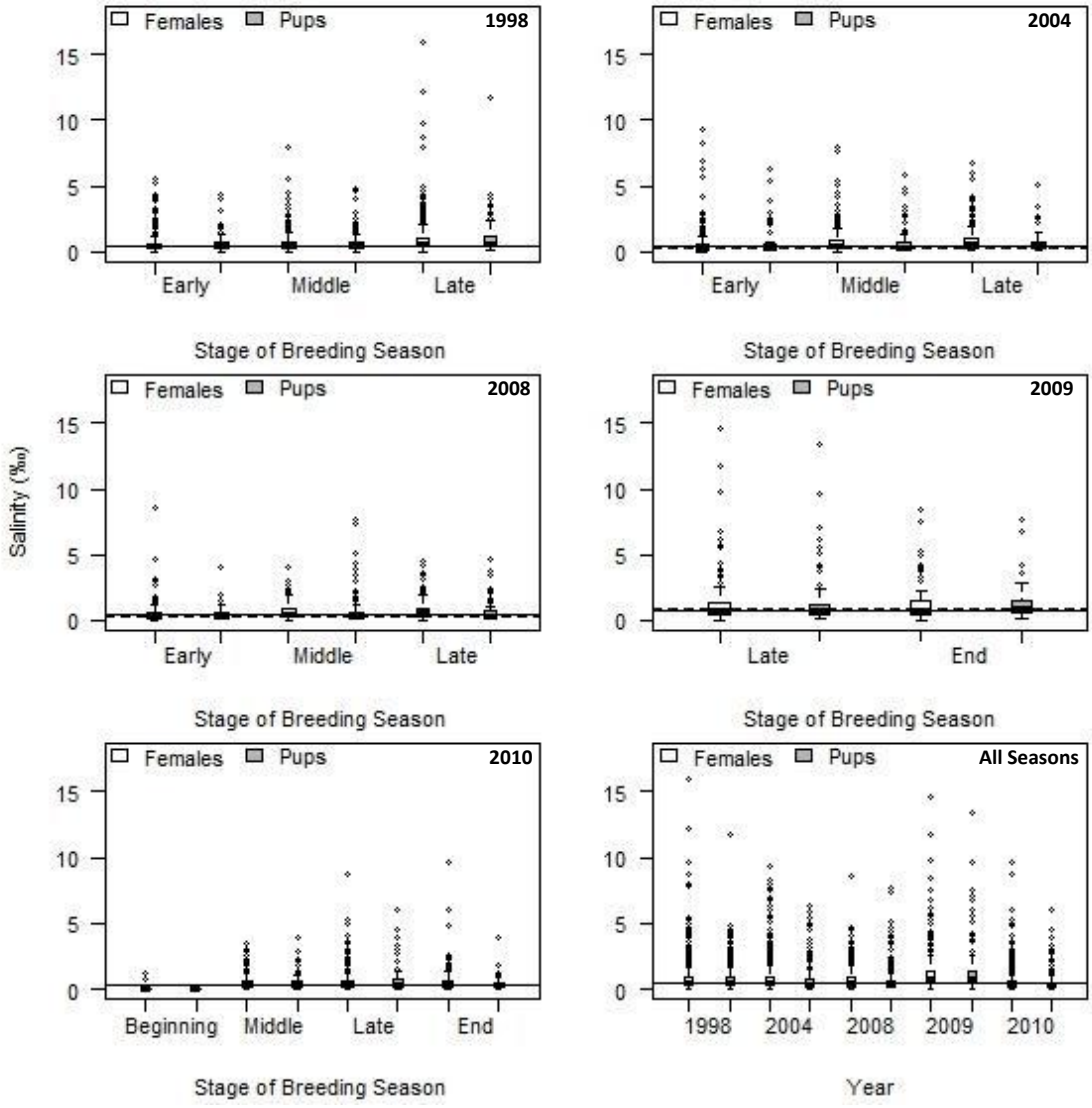


Figure A2.19: Female and pup distribution on salinity values (‰) during each breeding season stage. On all graphs the horizontal dashed line represents the pup median over the season and the solid horizontal line represents the female median.

Table A2.14: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in SAL values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	1.79	0.174
1998early-1998late	6.08	< 0.001
1998mid-1998late	-4.72	< 0.001
2004 early -2004 mid	5.08	< 0.001
2004early -2004late	5.40	< 0.001
2004mid -2004late	0.72	0.747
2008early-2008mid	6.05	< 0.001
2008early-2008late	5.40	< 0.001
2008mid-2008late	-0.24	0.968
2009late-2009end	0.05	0.962
2010beginning-2010mid	11.12	< 0.001
2010beginning-2010late	10.74	< 0.001
2010beginning-2010end	9.20	< 0.001
2010mid-2010late	0.06	1
2010mid-2010end	0.01	1
2010late-2010end	-0.04	1

Table A2.15: Results of MULTCOMP post-hoc multiple comparison tests of between-stage changes in SAL values at pup locations.

Comparison	t-value	*p*
1998early-1998mid	0.30	0.953
1998early-1998late	4.27	< 0.001
1998mid-1998late	4.56	< 0.001
2004 early -2004 mid	-0.49	0.873
2004early -2004late	0.12	0.993
2004mid -2004late	0.92	0.620
2008early-2008mid	0.97	0.593
2008early-2008late	1.43	0.325
2008mid-2008late	0.61	0.813
2009late-2009end	0.99	0.326
2010beginning-2010mid	12.83	< 0.001
2010beginning-2010late	9.89	< 0.001
2010beginning-2010end	8.14	< 0.001
2010mid-2010late	1.17	0.630
2010mid-2010end	0.12	0.999
2010late-2010end	-0.84	0.824

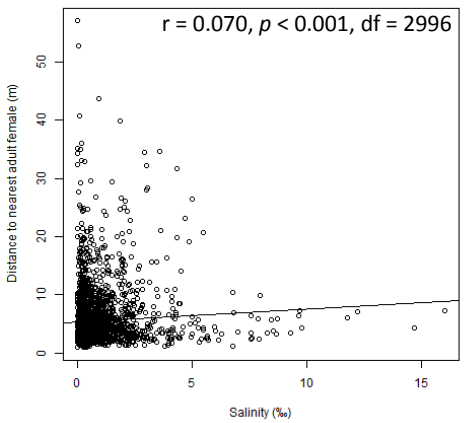


Figure A2.20: Correlation of salinity values with nearest neighbour distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows little relationship between the salinity of sites occupied by females and the distance to their nearest neighbour.

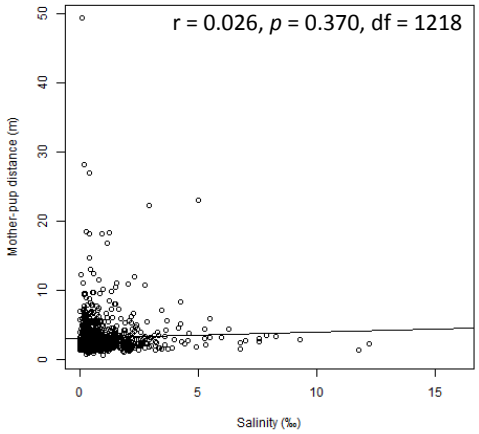


Figure A2.21: Correlation of salinity values with mother-pup distances of individual females across all breeding season, using data from focal days only. Pearson's product-moment correlation shows no relationship between the salinity of sites occupied by females and the distance to 'their' pup.

Appendix 3: Appendix to Chapter 4

Table A3.1: Summary of niche overlap statistics for females and pups on focal days throughout all five breeding seasons. Niche overlap between females and pups was assessed using Pianka's overlap index, *O*.

Year	EGV	Stage of Breeding Season				
		Beginning	Early	Middle	Late	End
1998	CACC	-	0.906	0.942	0.928	-
	CPOOL	-	0.954	0.948	0.866	-
	SAL	-	0.982	0.997	0.983	-
2004	CACC	-	0.810	0.948	0.894	-
	CPOOL	-	0.913	0.983	0.945	-
	SAL	-	0.961	0.991	0.994	-
2008	CACC	-	0.795	0.905	0.892	-
	CPOOL	-	0.889	0.985	0.938	-
	SAL	-	0.994	0.994	0.966	-
2009	CACC	-	-	-	0.900	0.764
	CPOOL	-	-	-	0.926	0.974
	SAL	-	-	-	0.985	0.961
2010	CACC	0.711	-	0.925	0.880	0.750
	CPOOL	0.966	-	0.981	0.944	0.891
	SAL	1.000	-	0.981	0.974	0.922

Table A3.2: Results of habitat suitability map validation using the Continuous Boyce Index (CBI). No ENFA was carried out for pups in the first stage in 2010, so no habitat suitability map exists to validate. Those results which show good model performance are highlighted in bold*.

Year	Stage of Breeding Season	Seal Class	CBI (Mean ± SD)
1998	Early	Female	**0.969 ± 0.024**
		Pup	0.250 ± 0.380
	Mid	Female	0.071 ± 0.201
		Pup	0.651 ± 0.328
	Late	Female	0.525 ± 0.310
		Pup	0.695 ± 0.214
2004	Early	Female	**0.818 ± 0.115**
		Pup	0.568 ± 0.393
	Mid	Female	**0.789 ± 0.023**
		Pup	**0.666 ± 0.062**
	Late	Female	**0.691 ± 0.124**
		Pup	0.441 ± 0.506
2008	Early	Female	0.191 ± 0.243
		Pup	0.444 ± 0.410
	Mid	Female	**0.843 ± 0.148**
		Pup	**0.800 ± 0.126**
	Late	Female	**0.645 ± 0.027**
		Pup	-0.361 ± 0.038
2009	Late	Female	0.313 ± 0.457
		Pup	0.623 ± 0.312
	End	Female	0.209 ± 0.588
		Pup	0.329 ± 0.275
2010	Beginning	Female	**0.747 ± 0.240**
		Pup	N/A
	Mid	Female	**0.907 ± 0.002**
		Pup	**0.964 ± 0.003**
	Late	Female	0.581 ± 0.127
		Pup	0.399 ± 0.222
	End	Female	**0.599 ± 0.027**
		Pup	0.007 ± 0.427

* Model performance judged by JES based on CBI and the colour coded system implemented in BioMapper which indicates the quality of model performance based on validation results.

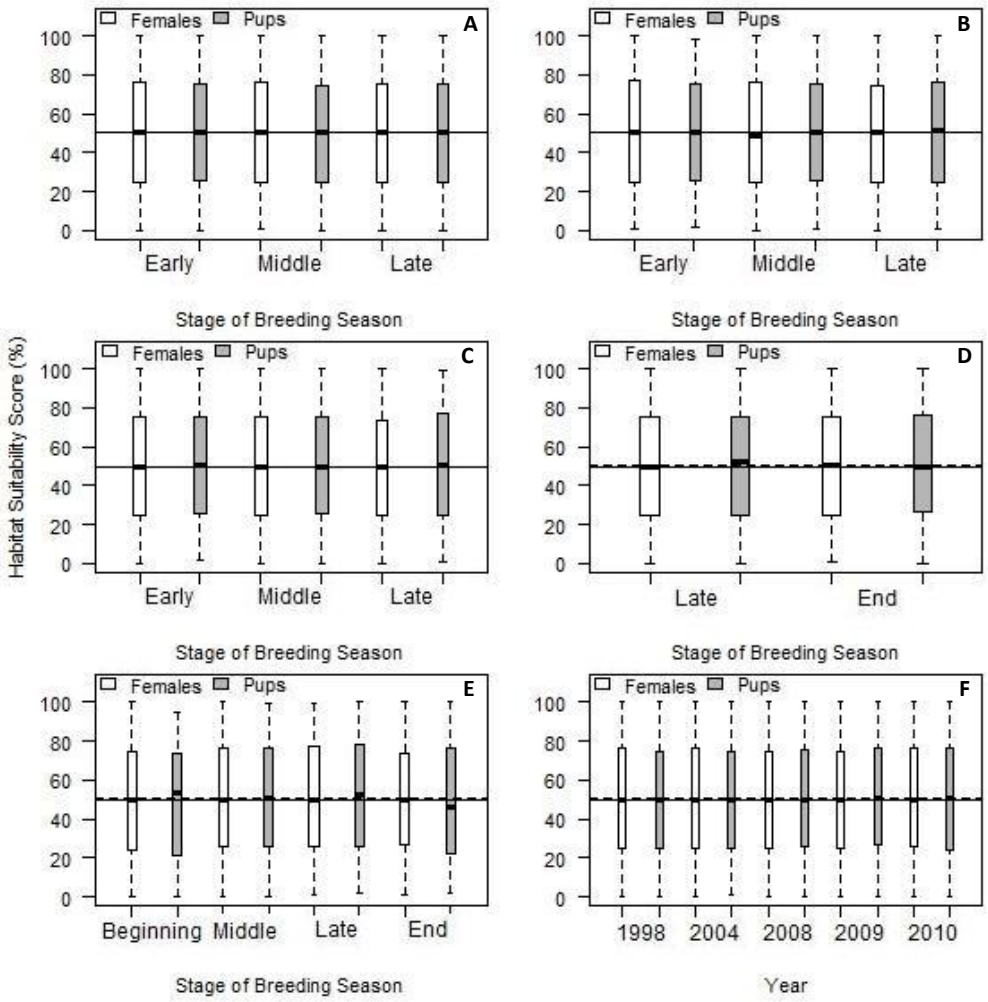


Figure A3.1: Female and pup habitat suitability scores for every focal day throughout each breeding season. **A:** 1998; **B:** 2004; **C:** 2008; **D:** 2009; **E:** 2010; **F:** All years, averaged across the season. The solid horizontal line represents the yearly (A-E) and overall (F) median HS for females, whilst that for pups is represented by the dashed horizontal line. Habitat suitability shown for pups at the beginning of 2010 for comparison only, as ENFA results indicated an anomalously large eigenvalue, so this ENFA and HS mapping iteration was not included in further analyses.

Appendix 4: Appendix to Chapter 5

Table A4.1: Summary of daily mean nearest Stage I-II pup neighbour distances ($\bar{d}_{obs}$) compared to $\bar{d}_{ran}$ and $\bar{d}_{dis}$ for each day during 2010. Day 1 = 28th September.

Day	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	Day	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$
1	11.28	38.32	82.35	**20**	9.92	15.74	33.82
2	10.58	33.79	72.62	**21**	10.94	16.90	36.31
3	9.82	32.89	70.69	**22**	11.89	17.14	36.83
4	13.81	32.06	68.90	**23**	9.92	17.39	37.36
5	13.81	29.27	62.89	**24**	10.22	17.39	37.36
6	12.37	25.75	55.34	**25**	10.99	16.03	34.45
7	10.53	21.61	46.45	**26**	11.91	17.65	37.93
8	12.29	21.86	46.99	**27**	12.76	18.67	40.11
9	10.13	19.33	41.55	**28**	12.40	18.21	39.13
10	9.55	17.65	37.93	**29**	11.52	19.33	41.55
11	9.87	17.26	37.09	**30**	14.72	20.28	43.57
12	9.53	15.28	32.85	**31**	13.20	19.33	41.55
13	8.97	15.11	32.48	**32**	14.54	20.48	44.02
14	8.42	15.20	32.66	**33**	16.77	19.88	42.73
15	9.03	15.46	33.23	**34**	15.04	19.69	42.32
16	8.07	15.20	32.66	**35**	14.93	19.69	42.32
17	7.99	15.28	32.85	**36**	17.42	21.14	45.43
18	8.96	15.28	32.85	**37**	17.87	22.39	48.12
19	8.07	16.45	35.34	**38**	-	-	-

Table A4.2: Summary of daily mean nearest Stage V pup neighbour distances ($\bar{d}_{obs}$) compared to $\bar{d}_{ran}$ and $\bar{d}_{dis}$ for each day during 2010. Day 1 = 28th September.

Day	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$	Day	$\bar{d}_{obs}$	$\bar{d}_{ran}$	$\bar{d}_{dis}$
1	-	-	-	**20**	31.62	43.23	92.90
2	-	-	-	**21**	35.94	45.34	97.44
3	-	-	-	**22**	18.45	45.34	97.44
4	-	-	-	**23**	17.63	38.32	82.35
5	-	-	-	**24**	23.76	45.34	97.44
6	-	-	-	**25**	17.67	37.02	79.56
7	-	-	-	**26**	15.60	35.84	77.03
8	-	-	-	**27**	18.10	31.29	67.24
9	-	-	-	**28**	23.25	27.09	58.23
10	-	-	-	**29**	15.16	29.90	64.25
11	-	-	-	**30**	12.31	21.86	46.99
12	-	-	-	**31**	12.15	17.78	38.22
13	-	-	-	**32**	13.70	18.21	39.13
14	-	-	-	**33**	12.37	19.88	42.73
15	-	-	-	**34**	11.84	19.33	41.55
16	25.39	143.37	308.12	**35**	10.24	18.67	40.11
17	25.32	101.38	217.87	**36**	10.03	19.33	41.55
18	26.82	82.78	177.89	**37**	31.62	17.14	36.83
19	17.09	50.69	108.94	**38**	-	-	-

Table A4.3 summarises the values for the nearest neighbour index, *R*, calculated for each day of 2010. The change in *R* indicates that Stage V are initially clustered and become more so as the season progresses. Tables A1.1 and A1.2 provide critical values for two methods of assessing the significance of *R*, as discussed in Section 3.2.3.

To provide a more concise measure of pattern, the nearest neighbour index '*R*' was calculated for each day using the locations of Stage I-II and Stage V pups (Tables A4.3 and A4.4). Values of *R* can range between 0.00 (complete clustering, NNdis = 0.00) and 2.15 (complete dispersion; maximum possible distance between each point, dependent on number of points within the study site), with a random pattern indicated by *R* = 1.00.

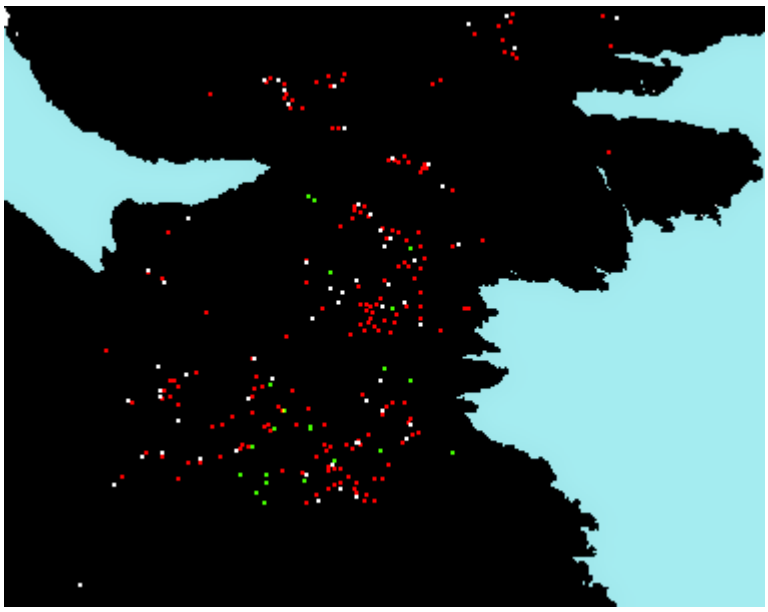
Table A4.3: Stage I-II pup nearest-neighbour index, R, values calculated for each day of 2010. See Figure 5.2 in Chapter 5.3.1. Day 1 = 28th September.

Day	R	Day	R	Day	R	Day	R
1	0.294	**11**	0.572	**21**	0.648	**31**	0.683
2	0.313	**12**	0.623	**22**	0.694	**32**	0.710
3	0.298	**13**	0.594	**23**	0.571	**33**	0.844
4	0.431	**14**	0.554	**24**	0.588	**34**	0.764
5	0.472	**15**	0.584	**25**	0.686	**35**	0.758
6	0.480	**16**	0.531	**26**	0.675	**36**	0.824
7	0.487	**17**	0.523	**27**	0.684	**37**	0.798
8	0.562	**18**	0.586	**28**	0.681	**38**	-
9	0.524	**19**	0.491	**29**	0.596		
10	0.541	**20**	0.630	**30**	0.726		

Table A4.4: Stage V pup nearest-neighbour index, R, values calculated for each day of 2010. See Figure 5.2 in Chapter 5.3.1. Day 1 = 28th September.

Day	R	Day	R	Day	R	Day	R
1	-	**11**	-	**21**	0.697	**31**	0.692
2	-	**12**	-	**22**	0.793	**32**	0.667
3	-	**13**	-	**23**	0.481	**33**	0.689
4	-	**14**	-	**24**	0.389	**34**	0.639
5	-	**15**	-	**25**	0.642	**35**	0.634
6	-	**16**	-	**26**	0.493	**36**	0.530
7	-	**17**	0.250	**27**	0.499	**37**	0.585
8	-	**18**	0.306	**28**	0.668	**38**	-
9	-	**19**	0.529	**29**	0.778		
10	-	**20**	0.395	**30**	0.694		

A



B

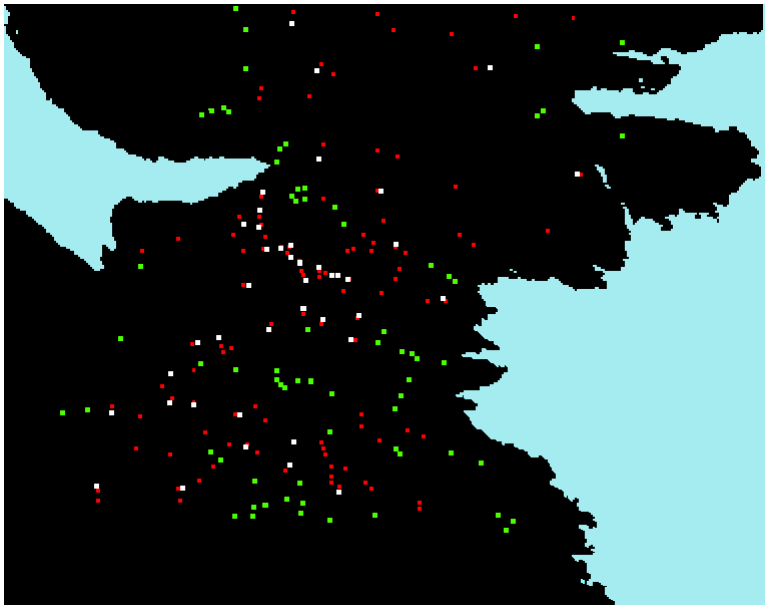


Figure A4.1: Distribution maps for **A:** Late and **B:** End 2010 for females (red), Stage I-II (white) and Stage V (green) pups on North Rona. Points enlarged (×4) for clarity. Unlike Stage I-II pups, Stage V pups are typically found in areas without females towards the outskirts of the colony, particularly towards the end of the season.

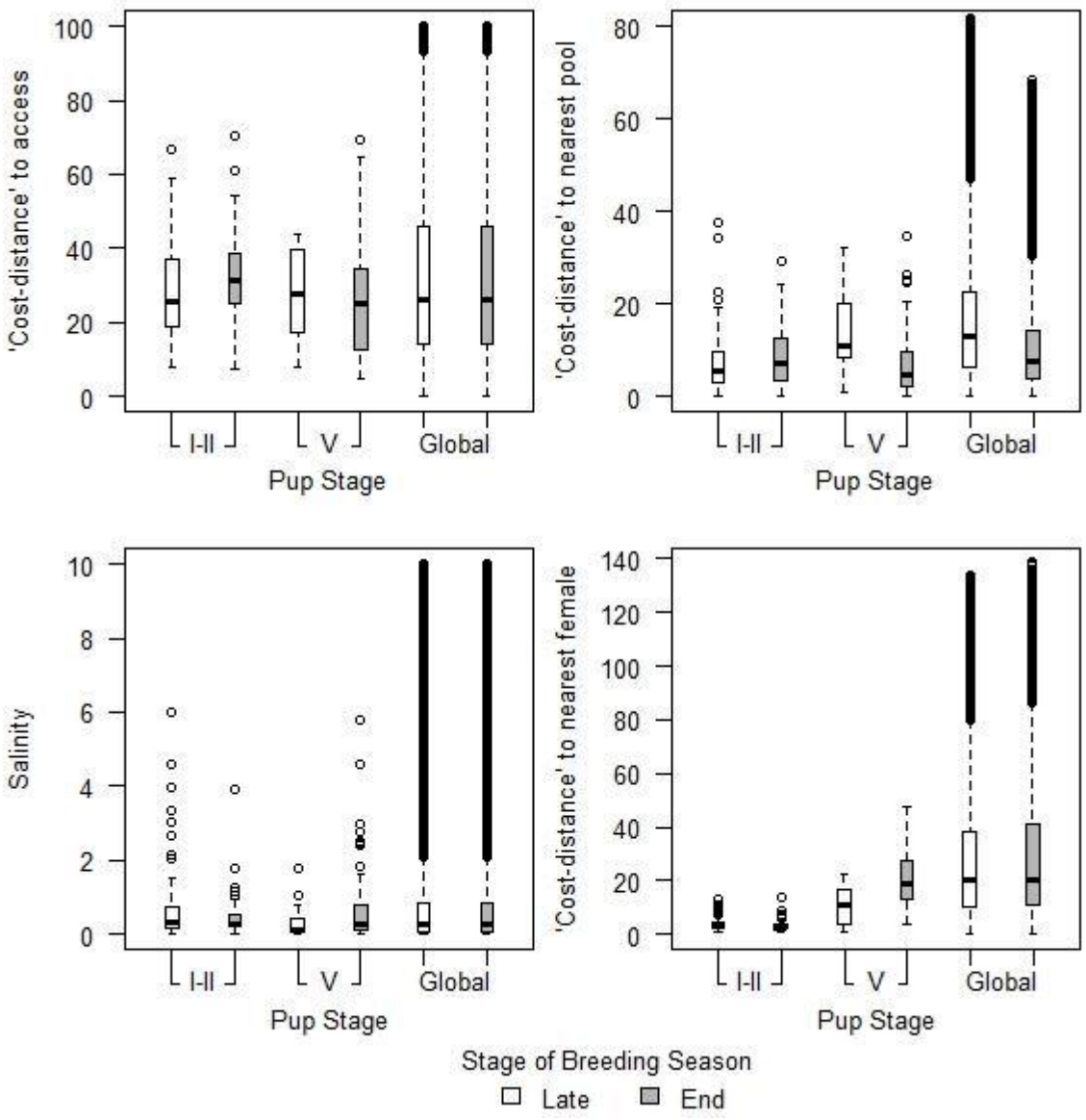


Figure A4.2: Stage I-II and Stage V pup distributions on each EGV (CACC, CPOOL, SAL and CFEM) for both focal dates during 2010, compared with the global distribution of each EGV. Equivalent to Figure 5.5, including 'outliers'.